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Acoustic communication in grasshopper communities (Orthoptera: Acrididae: Gomphocerinae): segregation of acoustic niches

Акустическая коммуникация в сообществах саранчовых (Orthoptera: Acrididae: Gomphocerinae): разделение акустических ниш

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KEY WORDS: grasshoppers, Acrididae, Gomphocerinae, songs, signals, communities, acoustic communication, communication channels, Russia.

КЛЮЧЕВЫЕ СЛОВА: саранчовые, Acrididae, Gomphocerinae, сигналы, сообщество, акустическая коммуникация, каналы связи, Россия.

ABSTRACT. Comparative study of calling signals in the communities of grasshoppers of the subfamily Gomphocerinae (Orthoptera: Acrididae) in European Russia, South Siberia and the Russian Far East was conducted. Different kinds of variability of signals were investigated. General structure of signals (single echeme or echeme-sequence), temporal pattern of syllables and their repetition period were demonstrated to be most constant characters and, consequently, most reliable when used in systematics. Combination of these characters provides for each species its own "place" in the acoustic environment of the community, so-called acoustic niche, which is a part of the ecological niche as a whole. Species producing similar signals, i.e. occupying the same acoustic niche are always either allopatric or inhabit different biotopes and thus avoid competition for acoustic communication channels.

РЕЗЮМЕ. Проведено сравнительное исследование призывных сигналов в сообществах саранчовых подсемейства Gomphocerinae (Orthoptera: Acrididae) в европейской части России, в Южной Сибири и на Дальнем Востоке. Исследованы различные типы изменчивости сигналов. Показано, что наиболее стабильными и, следовательно, надёжными при использовании в систематике признаками являются общая схема структуры сигнала (одиночные или периодически повторяющиеся фразы), временнóй рисунок серий и период их повторения. Сочетание этих признаков обеспечивает каждому виду определённое "место" в акустическом фоне сообщества, так называемую акустическую нишу, представляющую собой одну из составных частей экологической ниши в целом. Виды, издающие сходные сигналы, т.е. занимающие одну акустическую нишу, всегда оказываются аллопатрическими или населяют разные биотопы и, таким образом, избегают конкуренции за каналы акустической связи.

Introduction

Successful intraspecific communication in multispecies communities is impossible without partitioning of communication channels. Presently, it is known that competition for acoustic transmission channels between sympatric species ' actually exists in almost every more or less diverse taxonomic group of insects such as crickets, katydids (Orthoptera: Gryllidae and Tettigoniidae) and singing cicadas (Homoptera: Cicadidae). Moreover, every higher taxon as a whole has its distinct acoustic appearance thus occupying his own place in the acoustic environment of the biotope [Riede, 1996].

Until recently the most part of studies of acoustic communication in insect communities was performed on singing cicadas. It was found that in addition to differences in physical characteristics of the songs, i.e. their frequency spectra and/or temporal patterns these insects as a rule also demonstrate temporal and spatial segregation. First, different species prefer different calling sites, e.g. thin twigs or tree trunks and sing on different heights above the ground level [Claridge et al., 1979; Sueur, 2002]. Second, although most of species sing at various times during the day, peaks of their acoustic activity overlap only partially if ever [Sueur, 2002]. Third, in certain cases seasonal differences also

contribute segregation of sympatric species [Wolda, 1993; Sueur & Puissant, 2002]. Similar results were obtained for many species of vertebrates (birds, frogs) [e.g. Ficken et al., 1974; Hodl, 1977], but here we shall not go into details of these works.

In sympatric species of Gomphocerinae grasshoppers (Orthoptera: Acrididae) situation is somewhat different. Representatives of this group are most diverse in open landscapes of Palaearctic, i.e. steppes, semideserts or meadows in river valleys. Spatial structure of such biotopes is rather simple due to the absence of trees, and the potentialities of segregation of different species in the uniform area of grassland are rather low. Moreover, since the warm season on the most part of the territory of Palaearctic, especially, in the inner regions with continental climate is rather short, almost all species of Gomphocerinae have the same seasonality. Usually they emerge in the middle of June and sing until the end of August. The only example of seasonal segregation of two species of Gomphocerinae was described by Savitsky [2000]. For these reasons acoustic transmission channels in grasshopper communities sometimes are so "densely packed" that the signals of certain species differ from each other only in one physical parameter being almost identical in other characteristics.

In the first work on acoustic communication in grasshopper communities the authors proposed that partitioning of communication channels in sympatric Gomphocerinae is accomplished mainly via the differences in the repetition period of uniform elements of signals i.e. syllables [Bukhvalova & Zhantiev, 1994]. Later it was shown that real situation is somewhat more complicated and segregation of "acoustic niches" in these insects is accomplished due to differences in several parameters of the song [Bukhvalova, 2006]. This has been demonstrated by the examples of grasshopper community in Southern Tyva (South Siberia) and of certain species from the Lower Volga Region.

The aim of the present paper is to provide more detailed descriptions of further examples of acoustic segregation within grasshopper communities in several regions of Russia with regard to the variability of signal temporal parameters.

Materials and methods

Recordings of the songs were made under natural conditions from caged or freely-moving insects with microphone MD-382 (upper frequency limit 12.5 kHz) and cassette recorder Elektronika-302-1 (upper frequency limit 10 kHz) or minidisk recorder Sony Walkman MZ-NH900 (sampling frequency 44.1 kHz). In all cases manual mode of recording level control was used. Air temperature was measured during or immediately after recording on the place where the singing insect was sitting.

For estimation of probability of identity of syllables repetition period (SRP) in different songs Wilcoxon test was used. The specimens whose signals were recorded are deposited in the collection of the Zoological Museum of Moscow State University. Song terminology used in the present paper is accepted after the works by Ragge (e.g. Ragge, 1987); it is also used in our articles [Bukhvalova & Vedenina, 1998; Vedenina & Bukhvalova, 2001; Bukhvalova, 2006; Tishechkin, 2009; Tishechkin & Bukhvalova, 2009].

Data for recordings of calling signals presented on oscillograms (Figs 1–80) are given in the Table. Species both on Figs 1–68 and in the Table are arranged in the same order according to the temporal pattern of the songs and without considering their taxonomic relations. It should be pointed out, that for illustrations for each species most representative recordings of good quality were selected. For this reason the signals presented on oscillograms were not always recorded in the same locality and at the same temperature as ones used

Table. Data for recordings of calling signals of Gomphocerinae presented on oscillograms.
Таблица. Данные о записях призывных сигналов Gomphocerinae, представленных на осциллограммах.

Species	Locality and number of specimens	Air temperature during recording, °C
Omocestus petraeus (Brisout, 1855)	Rostov Area, Oblivskiy District, env. Sosnovy (= Oporny) village on Chir River.	27
Chorthippus vagans (Eversmann, 1848)	Rostov Area, Oblivskiy District, env. Sosnovy (= Oporny) village on Chir River.	28–30
Stenobothrus miramae Dirsh, 1931	Crimea, Kerchenskiy Peninsula, E shore of Kazantipskiy Bay, env. Zolotoe village.	29
Ch. macrocerus (Fischer-Waldheim, 1846)	Saratov Area, env. Khvalynsk Town, near Ulyanino village.	35
Ch. hammarstroemi (Miram, 1907)	Buryatia, the valley of Selenga River 5 km N of Novoselenginsk (20 km SSE of Gusinoozersk).	31–32
Aeropus sibiricus (Linnaeus, 1767)	Buryatia, 10 km E of Onokhoy village (about 60 km E of Ulan-Ude).	36
Glybtobothrus maritimus (Mistshenko, 1951)	Buryatia, Barguzin Depression, the valley of Ina River about 40 km NE of Barguzin Town.	20

Table. Continue.
Таблица. Продолжение.

Species	Locality and number of specimens	Air temperature during recording, °C
O. minutus (Brullé, 1832)	Rostov Area, Oblivskiy District, env. Sosnovy (= Oporny) village on Chir River.	27
G. mollis (Charpentier, 1825)	Saratov Area, env. Khvalynsk Town, near Ulyanino village.	32–33
Ch. apricarius (Linnaeus, 1758)	Rostov Area, Oblivskiy District, env. Sosnovy (= Oporny) village on Chir River.	28
Stauroderus scalaris (Fischer-Waldheim, 1846)	Buryatia, 10 km E of Onokhoy village (about 60 km E of Ulan-Ude) (Figs 23–24, 69).	36
	Saratov Area, env. Khvalynsk Town, near Ulyanino village (Figs 70–71).	32–33
Dasyhippus barbipes (Fischer-Waldheim, 1846)	Buryatia, 10 km E of Onokhoy village (about 60 km E of Ulan-Ude)	36
G. biguttulus (Linnaeus, 1758)	Moscow Area, Voskresensk District, env. Beloozerskiy Town.	27
O. viridulus (Linnaeus, 1758)	Moscow Area, Voskresensk District, env. Beloozerskiy Town.	26
O. haemorrhoidalis (Charpentier, 1825)	Saratov Area, env. Khvalynsk Town, near Ulyanino village.	35
Ch. parallelus (Zetterstedt, 1821)	Moscow Area, Voskresensk District, env. Beloozerskiy Town.	27
Mongolotettix japonicus japonicus (I. Bolivar, 1898)	South-west of Khabarovsk Province, about 5 km N of Obluchye Town.	25
Eremippus costatus Tarbinski, 1927	Volgograd.	29
Euchorthippus pulvinatus (Fischer-Waldheim, 1846)	South-East of Saratov Area, 10 km E of Ozinki Town.	35
Dociostaurus brevicollis (Eversmann, 1848)	Saratov Area, Krasnokutsky District, env. Dyakovka village.	33–34
Ch. dorsatus (Zetterstedt, 1821)	Moscow Area, Voskresensk District, env. Beloozerskiy Town.	33–34
Podismopsis genicularibus (Shiraki, 1910)	Amur Area, about 30 km W of Svobodny, env. Kostyukovka village (Figs 46–47).	25
	South-west of Khabarovsk Province, about 5 km N of Obluchye Town (Figs 48-49).	30
P. poppiusi (Miram, 1907)	Irkutsk Area, the valley of Uda River 10–12 km N of Nizhneudinsk.	28–30
P. ussuriensis micra Bey-Bienko, 1932	South-west of Khabarovsk Province, about 5 km N of Obluchye Town.	33–35
Chrysochraon dispar dispar (Germar, 1835)	Moscow Area, Voskresensk District, env. Beloozerskiy Town (Figs 72–73).	25–27
	Rostov Area, Oblivskiy District, env. Sosnovy (= Oporny) village on Chir River (Fig. 74).	30
Ch. dispar major Uvarov, 1925	South-west of Khabarovsk Province, about 5 km N of Obluchye Town.	33–35
Euthystira brachyptera (Ocskay, 1826)	South-west of Khabarovsk Province, about 5 km N of Obluchye Town.	33–35
Ch. intermedius (Bey-Bienko, 1926)	Buryatia, the valley of Irkut River 3-4 km W of Mondy village (80 km W of Kyren) (Figs 58–59).	26
	South-west of Khabarovsk Province, about 5 km N of Obluchye Town. (Figs 60–61).	33–35
S. nigromaculatus (Herrich-Schäffer, 1840)	Saratov Area, Krasnokutsky District, env. Dyakovka village.	33–34
Ch. karelini (Uvarov, 1910)	Irkutsk Area, the valley of Uda River 10–12 km N of Nizhneudinsk.	28–30
Ch. dichrous (Eversmann, 1859)	Saratov Area, Krasnokutsky District, env. Dyakovka village. (Figs 66–67).	29
	Volgograd (Fig. 68).	32–33

for obtaining data for histograms showing the distribution of SRP (Figs 86–100). Since the geographical variability of signal pattern within a subspecies or even a species in Gomphocerinae was not revealed [Vedenina & Bukhvalova, 2001; Tishechkin & Bukhvalova, 2009], this approach seems to be quite correct.

Results and discussion

1. Classification of grasshopper songs according to their temporal pattern

Signals of Gomphocerinae have wide-band noise frequency spectra widely overlapping in different species. Presently, there is no evidence of using frequency characteristics for recognition of conspecific signals in these insects [Meyer & Elsner, 1997]. For this reason in the following, only temporal pattern of signals will be considered.

Signals of grasshoppers consist of **syllables**, which are short uniform fragments of sound produced by one up-and-down stroke of hind leg. Syllables follow each other with more or less constant period and form an **echeme**. In certain species the song consists of single echemes separated by irregular intervals; in other ones echemes follow each other with more or less constant period and form an **echeme-sequence**.

On the first level of classification all signals studied can be subdivided into two main groups: single echemes and echeme-sequences. Single echemes last from 1.5–2 s up to about 1 minute in different species (Figs 1–33). Usually the male produces echemes with irregular intervals far exceeding the song in duration. In certain species the song normally includes two or three echemes separated by rather short pauses (Figs 5, 15, 27); the first echeme in this case as a rule is somewhat longer than the succeeding ones. Echeme-sequences in the most part of species normally last no less than 1–2 minutes and include 10–20 echemes and more (Figs 34–68). Not infrequently male can sing for about 10–15 minutes if not disturbed. True enough, in species producing single echemes individuals with unusually high acoustic activity sometimes sing with more or less regular intervals. On the other hand, forms producing echeme-sequences sometimes stop singing after emitting several echemes, especially when disturbed by wind or the presence of a man, etc. However, when observing a great number of singing individuals in nature one cannot but infer that these two types of songs actually exist.

The structure of syllables in Gomphocerinae is highly diverse and elaborated; nonetheless the most part of signals can be attributed to one of two main types according to this character. It should be noted that each type includes both single echemes and echeme-sequences.

The first type includes songs with syllables consisting of short discrete fragments separated by gaps (Figs 1–18 and 34–45). As a rule syllable begins quietly reaching maximum intensity near the middle or towards the end. Sometimes in the initial low-amplitude part of syllable prolonged fragment without gaps can be seen on oscillograms (Figs 8, 10, 16, 18, 35, 37).

The second type includes signals consisting of syllables without distinct gaps (Figs 29–33 and 50–65). As in the signals of the previous type, syllables usually begin quietly, reaching maximum intensity towards the end.

As a result four main groups are obtained. These are single echemes consisting of syllables with gaps (Figs 1–18), single echemes consisting of syllables without distinct gaps (Figs 29–33) and two groups of echeme-sequences consisting of syllables with gaps (Figs 34–45) and without gaps (Figs 50–65) respectively.

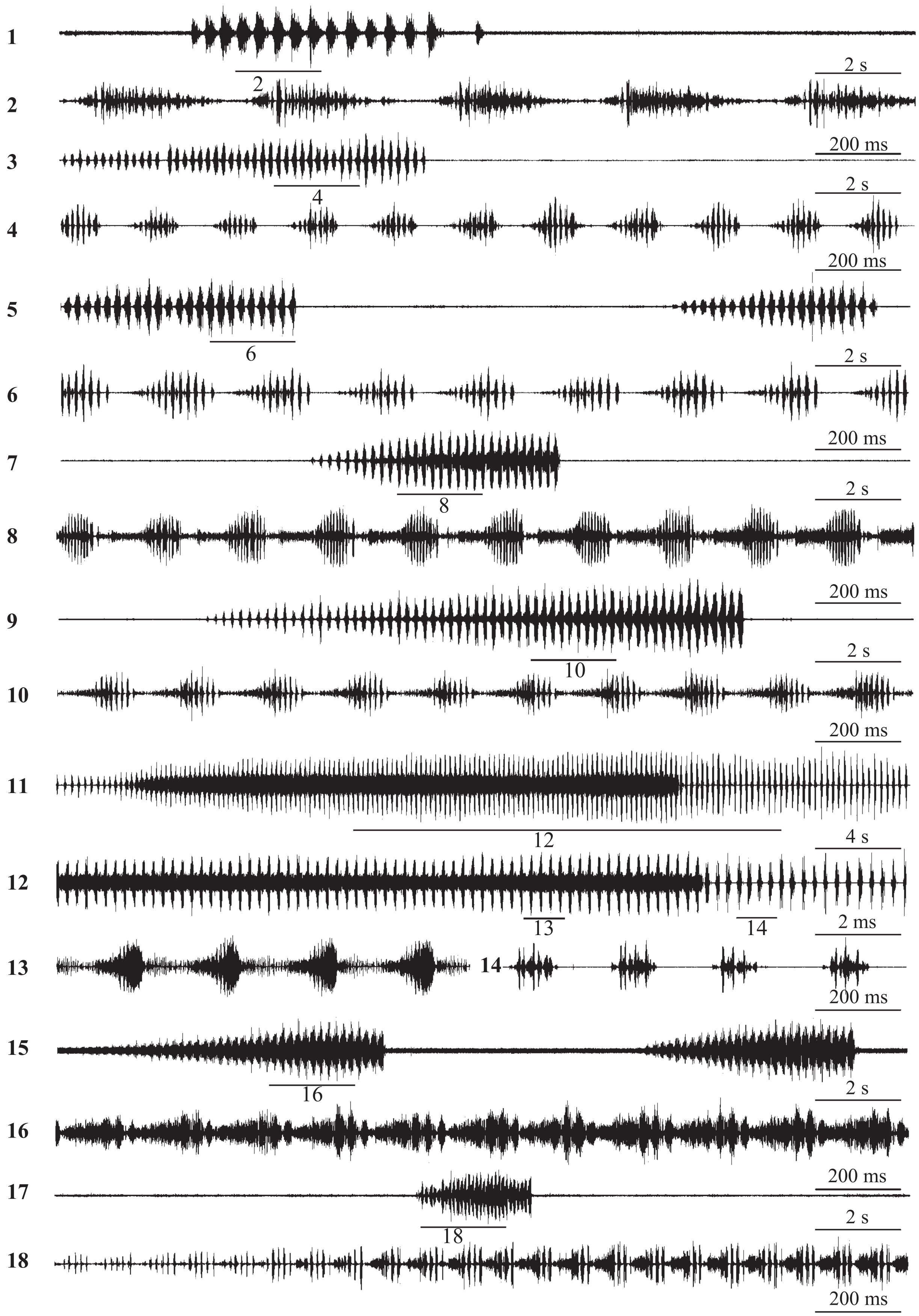
Signals with the structure of intermediate type are very rare. Occasionally the pattern of syllables changes gradually towards the end of signal: the gaps become less distinct and almost entirely disappear in the last syllables. Among species from the territory of Russia it is only known in *Chorthippus macrocerus* (Fischer-Waldheim, 1846) and in *Ch. hammarstroemi* (Miram, 1907) [Vedenina & Bukhvalova, 2001; Tishechkin & Bukhvalova, 2009]. However, the main part of such signals is composed of typical syllables with gaps (Figs 8, 10), so we attribute these songs to the first group (single echemes consisting of syllables with gaps). The situation with *Podismopsis genicularibus* (Shiraki, 1910) is more difficult. In different individuals the gaps in syllables are more or less distinct or even entirely absent (Figs 46–49), see also Tishechkin [2009]. For this reason on the scheme of distribution of SRP in different species we present two histograms for *P. genicularibus*, one for syllables with gaps, another for syllables without gaps. Similarly, in the song of *Ch. dichrous* (Eversmann, 1859) the gaps both within and between syllables usually are partially absent (Fig. 68). Only rarely in certain individuals the structure of the echeme becomes more distinct (Fig. 67). Thus, the song of this species is attributed to echeme-sequences consisting of syllables without gaps.

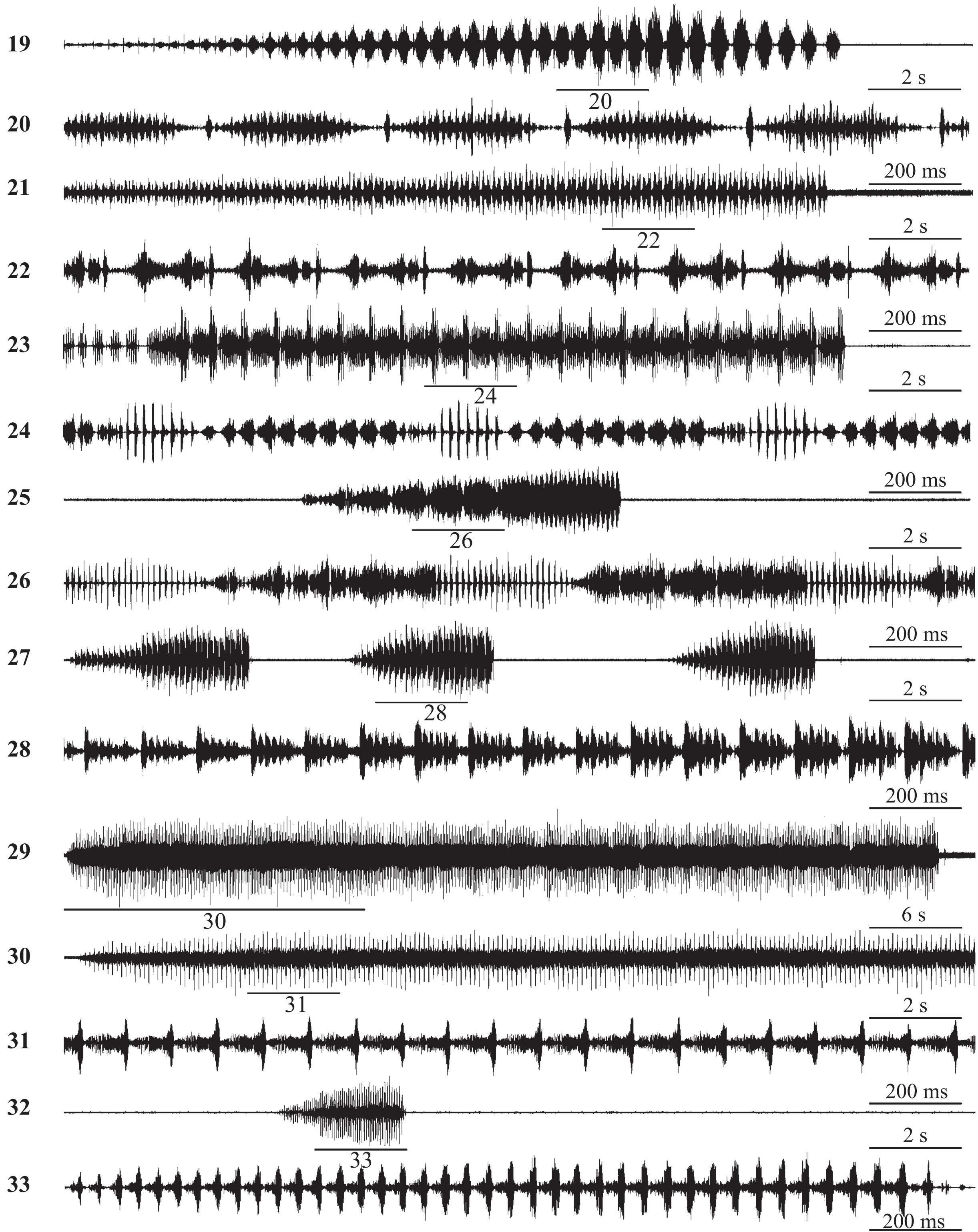
Also there are several species, which cannot be included into any of these groups.

First, these are *Glyptobothrus mollis* (Charpentier, 1825) and *Chorthippus apricarius* (Linnaeus, 1758). In both species the song is a single echeme consisting of

Figs 1–18. Oscillograms of calling signals of grasshoppers of the subfamily Gomphocerinae. 1–2 — *Omocestus petraeus*, 3–4 — *Chorthippus vagans*, 5–6 — *Stenobothrus miramae*, 7–8 — *Ch. macrocerus*, 9–10 — *Ch. hammarstroemi*, 11–14 — *Aeropus sibiricus*, 15–16 — *Glybtobothrus maritimus*, 17–18 — *O. minutus*. Faster oscillograms of the parts of signals indicated as “2”, “4”, “6”, “8”, “10”, “12–14”, “16” and “18” are given under the same numbers.

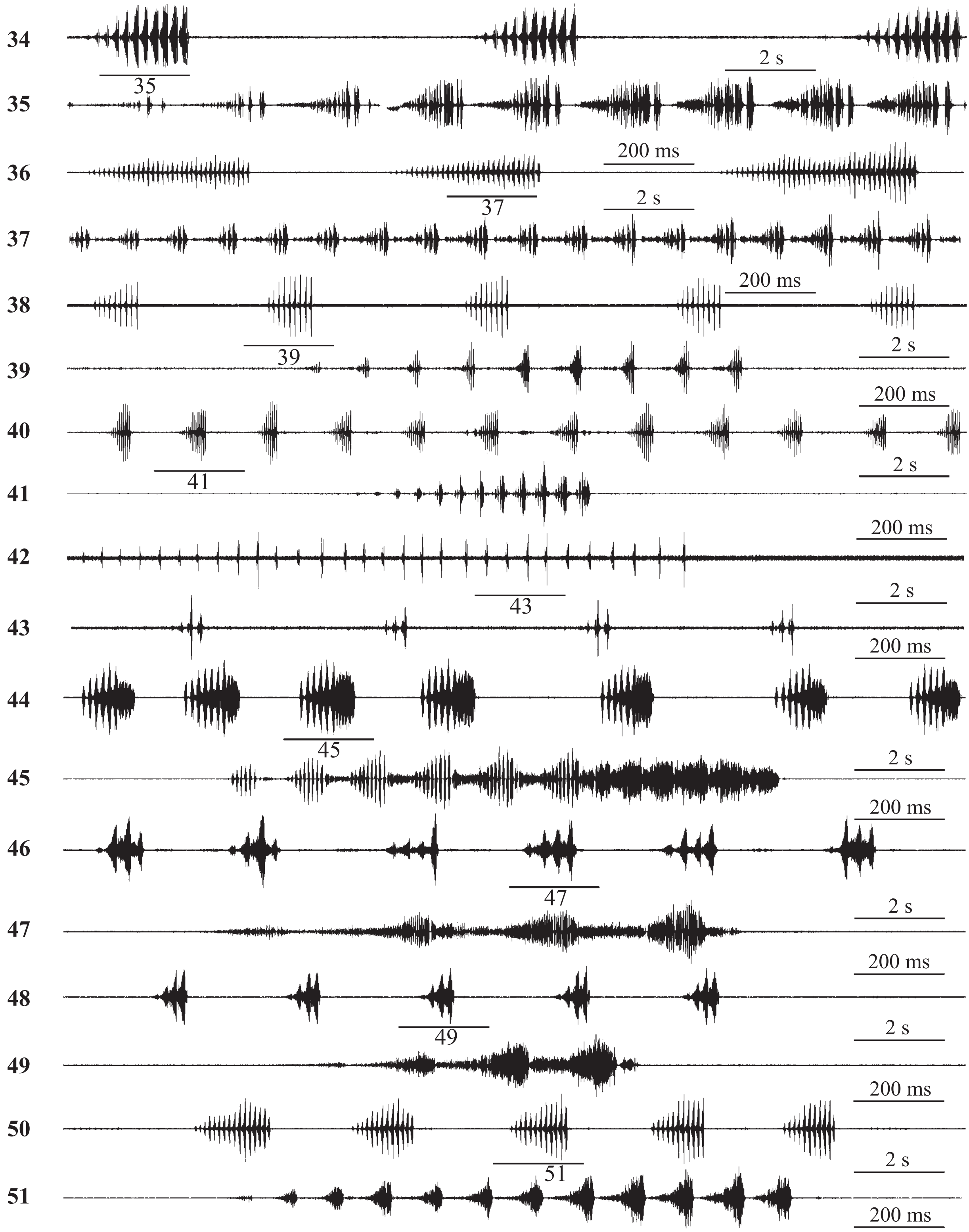
Рис. 1–18. Осциллограммы призывных сигналов саранчовых подсемейства Gomphocerinae. 1–2 — *Omocestus petraeus*, 3–4 — *Chorthippus vagans*, 5–6 — *Stenobothrus miramae*, 7–8 — *Ch. macrocerus*, 9–10 — *Ch. hammarstroemi*, 11–14 — *Aeropus sibiricus*, 15–16 — *Glybtobothrus maritimus*, 17–18 — *O. minutus*. Фрагменты сигналов, помеченные цифрами “2”, “4”, “6”, “8”, “10”, “12–14”, “16” и “18”, представлены при большей скорости развёртки на осциллограммах под такими же номерами.


1
2 s
2
2
200 ms
3
2 s
4
4
200 ms
5
6
2 s
6
200 ms
7
2 s
8
8
200 ms
9
2 s
10
10
200 ms
11
12
4 s
12
13
14
2 ms
13
14
200 ms
15
16
2 s
16
200 ms
17
2 s
18
18
200 ms



Figs 19–33. Oscillograms of calling signals of grasshoppers of the subfamily Gomphocerinae. 19–20 — *Glyptobothrus mollis*, 21–22 — *Chorthippus apricarius*, 23–24 — *Stauroderus scalaris*, 25–26 — *Dasyhippus barbipes*, 27–28 — *G. biguttulus*, 29–31 — *Omocestus viridulus*, 32–33 — *O. haemorrhoidalis*. Faster oscillograms of the parts of signals indicated as "20", "22", "24", "26", "28", "30–31" and "33" are given under the same numbers.

Рис. 19–33. Осциллограммы призывных сигналов саранчовых подсемейства Gomphocerinae. 19–20 — *Glyptobothrus mollis*, 21–22 — *Chorthippus apricarius*, 23–24 — *Stauroderus scalaris*, 25–26 — *Dasyhippus barbipes*, 27–28 — *G. biguttulus*, 29–31 — *Omocestus viridulus*, 32–33 — *O. haemorrhoidalis*. Фрагменты сигналов, помеченные цифрами "20", "22", "24", "26", "28", "30–31" и "33", представлены при большей скорости развёртки на осциллограммах под такими же номерами.



Figs 34–51. Oscillograms of calling signals of grasshoppers of the subfamily Gomphocerinae. 34–35 — *Chorthippus parallelus*, 36–37 — *Mongolotettix japonicus japonicus*, 38–39 — *Eremippus costatus*, 40–41 — *Euchorthippus pulvinatus*, 42–43 — *Dociostaurus brevicollis*, 44–45 — *Ch. dorsatus*, 46–49 — *Podismopsis genicularibus*, 50–51 — *P. poppiusi*. Faster oscillograms of the parts of signals indicated as “35”, “37”, “39”, “41”, “43”, “45”, “47”, “49” and “51” are given under the same numbers.

Рис. 34–51. Осциллограммы призывных сигналов саранчовых подсемейства Gomphocerinae. 34–35 — *Chorthippus parallelus*, 36–37 — *Mongolotettix japonicus japonicus*, 38–39 — *Eremippus costatus*, 40–41 — *Euchorthippus pulvinatus*, 42–43 — *Dociostaurus brevicollis*, 44–45 — *Ch. dorsatus*, 46–49 — *Podismopsis genicularibus*, 50–51 — *P. poppiusi*. Фрагменты сигналов, помеченные цифрами “35”, “37”, “39”, “41”, “43”, “45”, “47”, “49” и “51”, представлены при большей скорости развёртки на осциллограммах под такими же номерами.

syllables separated by short abrupt clicks (Figs 19–22). Patterns of syllables in two species are different, but in other characters their signals are similar.

Second, these are *Stauroderus scalaris* (Fischer-Waldheim, 1846) and *Dasyhippus barbipes* (Fischer-Waldheim, 1846) (Figs 23–26). The main parts of signals in both species are successions of elaborate fragments with similar structure (Figs 24 and 26). Formally, their songs should be attributed to echeme-sequences when the pattern of leg movements is considered. However, oscillograms of these signals in general appearance are similar with single echemes (Figs 1–22 and 23–26), but differ distinctly from typical echeme-sequences (Figs 34–68). In addition, it should be taken into consideration that insects using acoustic communication perceive the sounds, but not the movements of the parts of sound-producing apparatus.

Third, this is *G. biguttulus* (Linnaeus, 1758) (Figs 27–28). According to Ragge and Reynolds [1998], formally, the song of this species includes several echeme-sequences each consisting of echemes formed by three diplosyllables (= six hemisyllables). However, it is evident from the oscillograms that the pattern of sound (if not of leg movements) in this species is similar with these in single echemes of other ones (e.g. Figs 27–28 and 15–18). For this reason it can be attributed to signals consisting of single or irregularly repeated echemes.

In a small number of species of Gomphocerinae the echeme consists of two different parts. Sometimes additional part is not a necessary component of signal (Figs 58–61), but in other cases it is always present in the song (Figs 11–12, 44–45). In these cases we provide different histograms for each part on the schemes of distribution of SRP.

2. Variability of signal temporal pattern

Similarly to all other characters, temporal pattern of grasshopper songs demonstrate various kinds of variability.

Echemes as a rule consist of uniform or slightly variable syllables. Only in a small number of species (4 of 30 included in the present paper) echemes include successions of syllables of two different types. In *Aeropus sibiricus* (Linnaeus, 1767) (Figs 11–14) and *Chorthippus dorsatus* (Zetterstedt, 1821) (Figs 44–45) both parts are necessary components of a song. On the contrary, in *S. scalaris* and *Ch. intermedius* (Bey-Bienko, 1926) one of the components can be reduced entirely or partially. In the song of *S. scalaris* the initial part consists of irregularly repeated variable echemes. It can be well-developed (Fig. 69) or reduced to some extent (Figs 70–71); occasionally all the variants can be heard in the same individual. *Ch. intermedius* can produce echemes of two types consisting of one (Fig. 59) or two (Fig. 61) parts respectively. Usually the shape of echemes does not change within a song, but different songs of the same male sometimes differ from each other in echeme structure.

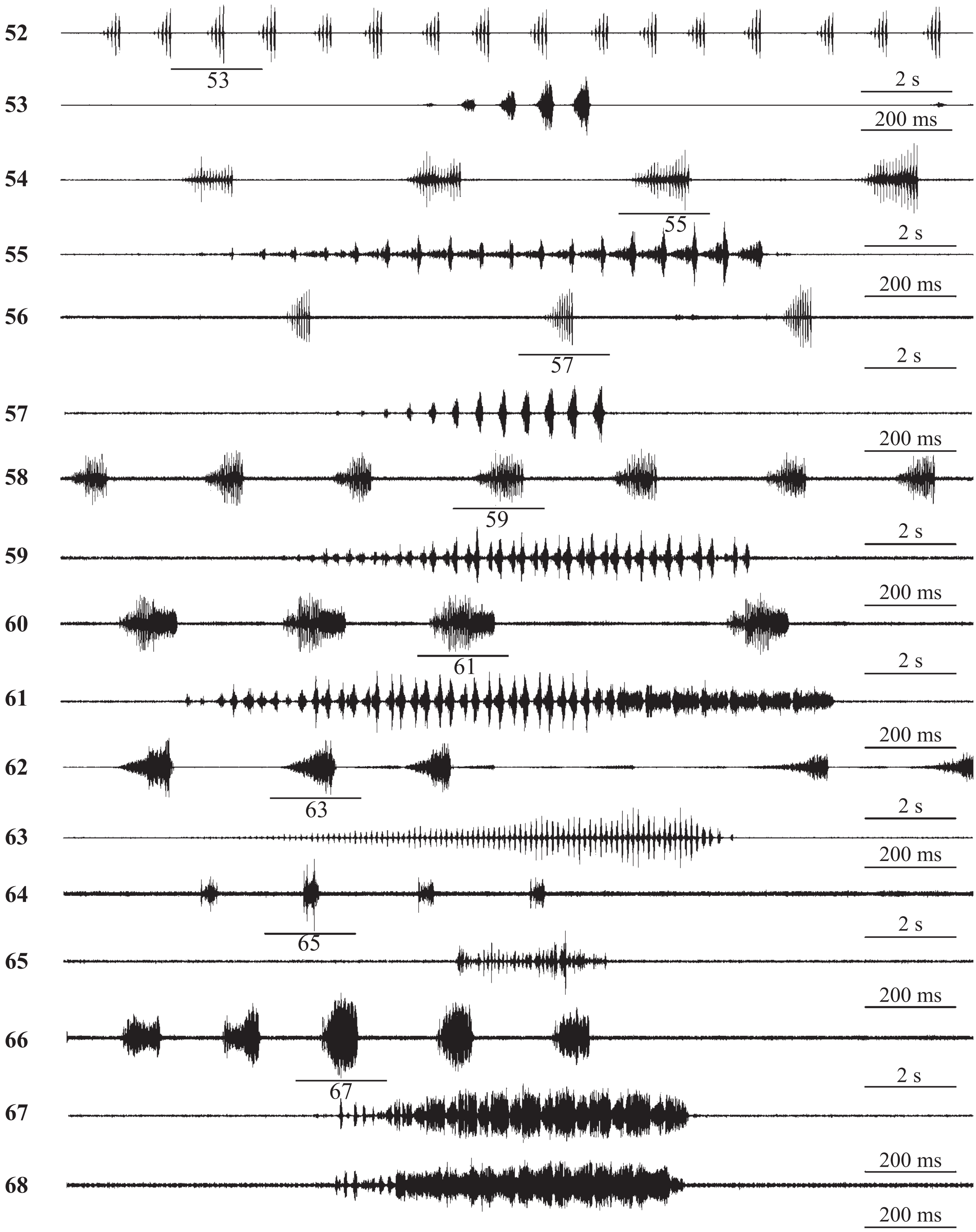
Temporal pattern of syllables for the most part is a constant species-specific character. Usually, the variability of their shape is limited to differences in amplitude relations of the components of syllable and to change of the number of gaps (Figs 72–74 and 75–76). Signals of the same male for the most part are indistinguishable from each other in the shape of syllables, but the songs of different individuals as a rule are somewhat different in this character. This is true even for the males from the same locality.

As mentioned above, gradual changes of syllable shape towards the end of signal in Gomphocerinae is a rare case. Only in *Ch. macrocerus* and *Ch. hammarstroemi* the last syllables in the echeme usually differ from these in the main part of the song due to reduced number or total absence of gaps (Figs 77–78; two fragments following immediately one after another are presented).

The variability of the structure of syllables resulting from differences in leg movements pattern was found only in *G. biguttulus*. Normally, the song of this species is a succession of repeated short fragments, each produced by three up-and-down strokes of hind legs. Therefore, according to Ragge and Reynolds [1998], each fragment consists of three diplosyllables. However, in individuals from Moscow Area fragments consisting of four diplosyllables occasionally present (Figs 79–80, in the end of the oscillograms). This indicates conclusively that occasionally male makes not three, but four strokes by hind legs during singing.

In the last decade several articles concerning comparative analysis of the songs of widespread species recorded in different localities in Russia and adjacent countries were published [Bukhvalova, 1997; Vedenina & Bukhvalova, 2001; Tishechkin, 2009; Tishechkin & Bukhvalova, 2009]. Investigation of songs of more than 20 species demonstrated that within a subspecies or monotypic species signal temporal pattern retains all its parameters over many hundreds or even thousands of kilometres of the range. Differences in temporal patterns of songs (usually in duration of echemes, more rarely in syllable pattern) were observed only between subspecies. The only exception is *P. genicularibus*. Morphological subspecies in this species were not described, but signals of individuals from the western part of the Russian Far East and from the Maritime Territory differ from each other in the duration of echemes on the same level as in good subspecies [Tishechkin, 2009].

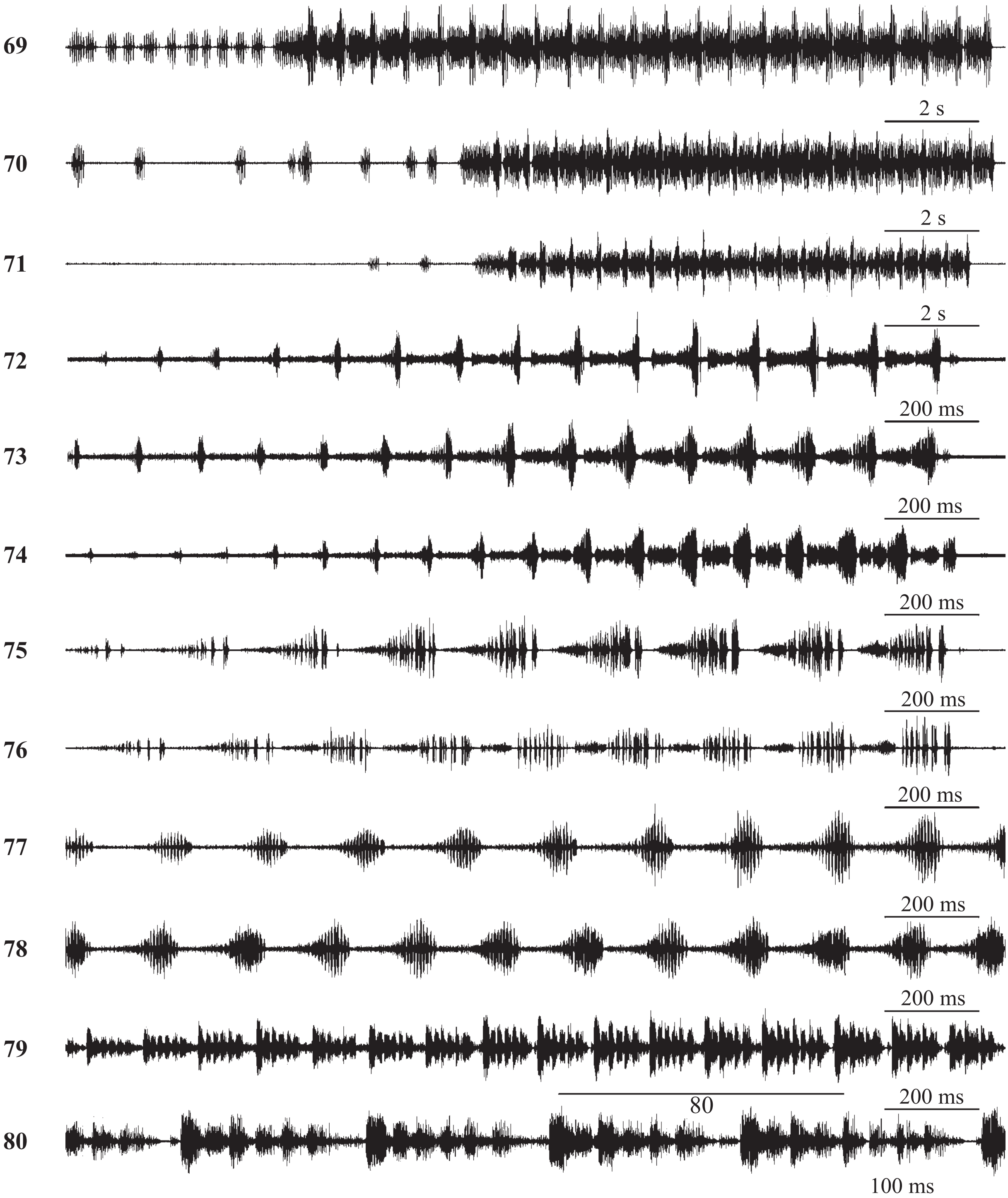
Duration of single echemes as well as an echeme repetition period in echeme-sequences can vary greatly. Disturbance caused by various reasons (approaching man, wind, presence of conspecific individuals, etc.) is a main factor affecting these parameters. Moreover, in most species of Gomphocerinae duration of echemes have close values (Figs 81–82). Species producing single echemes can be classified into two main groups. In *Ch. apricarius*, *S. scalaris* and certain other forms echeme duration usually averages 10–20 s and more (Fig. 81). In some other ones, like *Omocestus haemorrhoidalis* (Charpentier, 1825) and *O. petraeus* (Brisout, 1855), duration of songs does not exceed 5–7 s. Within each group the values of echeme duration overlap al-



Figs 52–68. Oscillograms of calling signals of grasshoppers of the subfamily Gomphocerinae. 52–53 — *Podismopsis ussuriensis micra*, 54–55 — *Chrysochraon dispar major*, 56–57 — *Euthystira brachyptera*, 58–61 — *Chorthippus intermedius*, 62–63 — *Stenobothrus nigromaculatus*, 64–65 — *Ch. karelini*, 66–68 — *Ch. dichrous*. Faster oscillograms of the parts of signals indicated as “53”, “55”, “57”, “59”, “61”, “63”, “65” and “67” are given under the same numbers.

Рис. 52–68. Осциллограммы призывных сигналов саранчовых подсемейства Gomphocerinae. 52–53 — *Podismopsis ussuriensis micra*, 54–55 — *Chrysochraon dispar major*, 56–57 — *Euthystira brachyptera*, 58–61 — *Chorthippus intermedius*, 62–63 — *Stenobothrus nigromaculatus*, 64–65 — *Ch. karelini*, 66–68 — *Ch. dichrous*. Фрагменты сигналов, помеченные цифрами “53”, “55”, “57”, “59”, “61”, “63”, “65” и “67”, представлены при большей скорости развёртки на осциллограммах под такими же номерами.

most completely; in addition, certain species occupy intermediate position between two groups in this character (e.g. *Ch. macrocerus*, Fig 81, the first histogram from the bottom). In species producing echeme-sequences echeme duration is more constant. However, even in sympatric species it can overlap to a great extent (Fig.



Figs 69–80. Oscillograms of calling signals of grasshoppers of the subfamily Gomphocerinae. 69–71 — *Stauroderus scalaris*, 72–74 — *Chrysochraon dispar dispar*, 75–76 — *Chorthippus parallelus*, 77–78 — *Ch. macrocerus* , two parts of the same signal following one immediately after another, 79–80 — *Glybtobothrus biguttulus*. Faster oscillogram of the part of signal indicated as "80" is given under the same number.

Рис. 69–80. Осциллограммы призывных сигналов саранчовых подсемейства Gomphocerinae. 69–71 — *Stauroderus scalaris*, 72–74 — *Chrysochraon dispar dispar*, 75–76 — *Chorthippus parallelus*, 77–78 — *Ch. macrocerus* , две части сигнала, следующие непосредственно одна за другой, 79–80 — *Glybtobothrus biguttulus*. Фрагмент сигнала, помеченный цифрой "80", представлен при большей скорости развёртки на осциллограмме под таким же номером.

82); the same is true for echeme repetition period.

SRP is more constant parameter of signal; nevertheless it also demonstrates different kinds of variability.

It is self-evident that SRP cannot be absolutely constant even over the same signal. In a number of species it only fluctuates about mean value, but in other ones its changes exhibit some regular trends. Usually it is observed in species producing prolonged single echemes. In *O. haemorrhoidalis*, *O. viridulus* (Linnaeus, 1758), *O. petraeus* and *Stenobothrus miramae* Dirsh, 1931 SRP gradually increases towards the end of the echeme (Fig. 83). In *Ch. apricarius* SRP gradually decreases over the most part of the signal and abruptly increases in the end (Fig. 84). Similar trend usually demonstrate *S. scalaris* and *O. minutus.* In certain species SRP retains more or less constant values throughout the most part of signal, but abruptly increases or decreases in the end. Abrupt increase of SRP sometimes is observed in the song of *G. mollis* (Fig. 85); decrease of SRP in the end of signal is characteristic for *Ch. macrocerus*. Therefore, for obtaining comprehensive data on the range of SRP the measurements should be made with due respect of the change of this parameter over the signal. Measurements in randomly selected or "most characteristic" fragments can cause an error.

It is common knowledge that repetition period of components of acoustic signals in insects decrease with increasing temperature. Analysis of signals of the same male recorded at different temperatures showed that grasshoppers are no exception. Even an increase of temperature of 2–3°C results in considerable changes of this parameter (Figs 86–87).

The values of SRP in different signals of the same individual recorded at the fixed temperature occupy approximately the same range (Fig. 88). On the other hand, the ranges of SRP in signals of different males singing at the same temperature usually overlap only partially if ever (Figs 88–89). Consequently, analysis of a small number of songs of several males provides more comprehensive data on SRP variability than analysis of many songs of the same male.

Geographical variability of SRP in Gomphocerinae was not revealed. The values of SRP occupy almost the same range even in individuals from the populations located at a distances of thousands kilometres from each other (e.g. from European Russia, Lower Volga Region and the Russian Far East, Figs 90–91).

Thus one can draw the conclusion that the pattern of syllables and SRP in the songs of Gomphocerinae are the most reliable diagnostic characters. On the other hand, the use of echeme duration and repetition period for species recognition is hardly possible.

3. Segregation of communication channels in grasshopper communities

Comparative investigations of calling signals of Gomphocerinae were performed in seven grasshopper communities in various regions of Russia. In each biotope an area about 10–20 m in diameter with more or less uniform vegetation was selected. Within this area signals of Gomphocerinae inhabiting the site and coming into acoustic interactions with each other were recorded. As a rule, the investigator remaining on the same place could hear the signals of all these species. Species composition of vegetation and proportions of singing individuals of different species were not studied. For comparison of temporal parameters recordings made at temperatures within the range of no more than 3°C were used. In each region signals of no less than 3–4 males of each species were analysed. The localities and biotopes, where our studies were conducted are listed below.

1. Moscow Area, Voskresensk Region, environs of Beloozerskiy Town, the meadow with mesophytic vegetation. Recordings of signals for comparative analysis of temporal parameters were made at the temperature 27–30°C.

2. Rostov Area, Oblivskiy District, env. Sosnovy (= Oporny) village on Chir River, meadow with rather diverse mesophytic vegetation on the edge of the field near Chir River. For comparative analysis recordings made at the temperature 27–30°C were used.

3. Same locality, glades on the edges or within the forest shelter-belts, consisting of oak and/or two species of pines. Recordings of signals were made at the temperature 27–30°C.

4. Same locality, steppe dominated by *Stipa* sp. and *Festuca* sp. (Poaceae). The studied fragment of steppe was situated on the slope on the bank of Chir River and remained unploughed for this reason. Signal recordings were made at the temperature 27–30°C.

5. Volgograd, saline land on the outskirts of the city. A number of partially dry salted pools with several concentric belts of vegetation around each of them. Inner belts were formed by halophylous Chenopodiaceae, then followed *Artemisia* spp. from the subgenus *Seriphidium* mixed with several species of Poaceae; on the outer edges vegetation graded into xerophytic steppe biotopes. Since in the belt of Chenopodiaceae grasshoppers were found only occasionally, we investigated signals of Gomphocerinae in the zone dominated by *Artemisia* subg. *Seriphidium.* Recordings of signals for comparative analysis were made at the temperature 27–30°C.

6. Irkutsk Area, Uda River near the mouth of Uk, about 30 km north-west of Nizhneudinsk (approx. 450 km north-west of Irkutsk), polydominant wet glade on the bank of Uk River. Recordings of signals were made at the temperature 28–31°C.

7. South-west of Khabarovsk Province, about 5 km north of Obluchye Town, small bog dominated by sedges (*Carex* spp.). Recordings of signals were made at the temperature 32–35°C.

The results of signal comparison are presented on the schemes arranged in the same manner for each grasshopper community (Figs 92–98). The values of SRP in the signals of each species are presented as a histogram. Histograms are classified into two main groups according to signal structure: single echemes in the lower part of a scheme and echeme-sequences in the upper part; each group is indicated by schematic drawing of corresponding oscillogram. Within each group

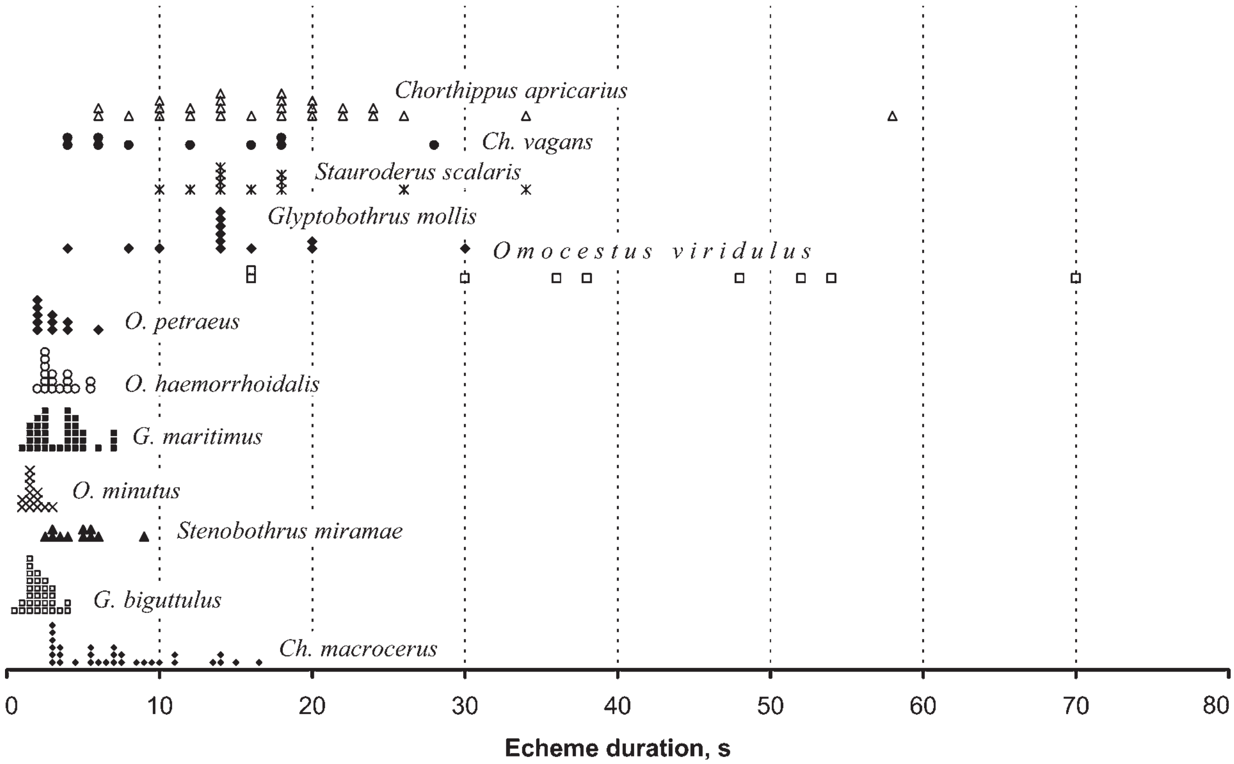


Fig. 81. Histograms of distribution of single echemes duration values in certain species of Gomphocerinae.

Рис. 81. Гистограммы распределения значений длительности одиночных фраз у некоторых видов Gomphocerinae.

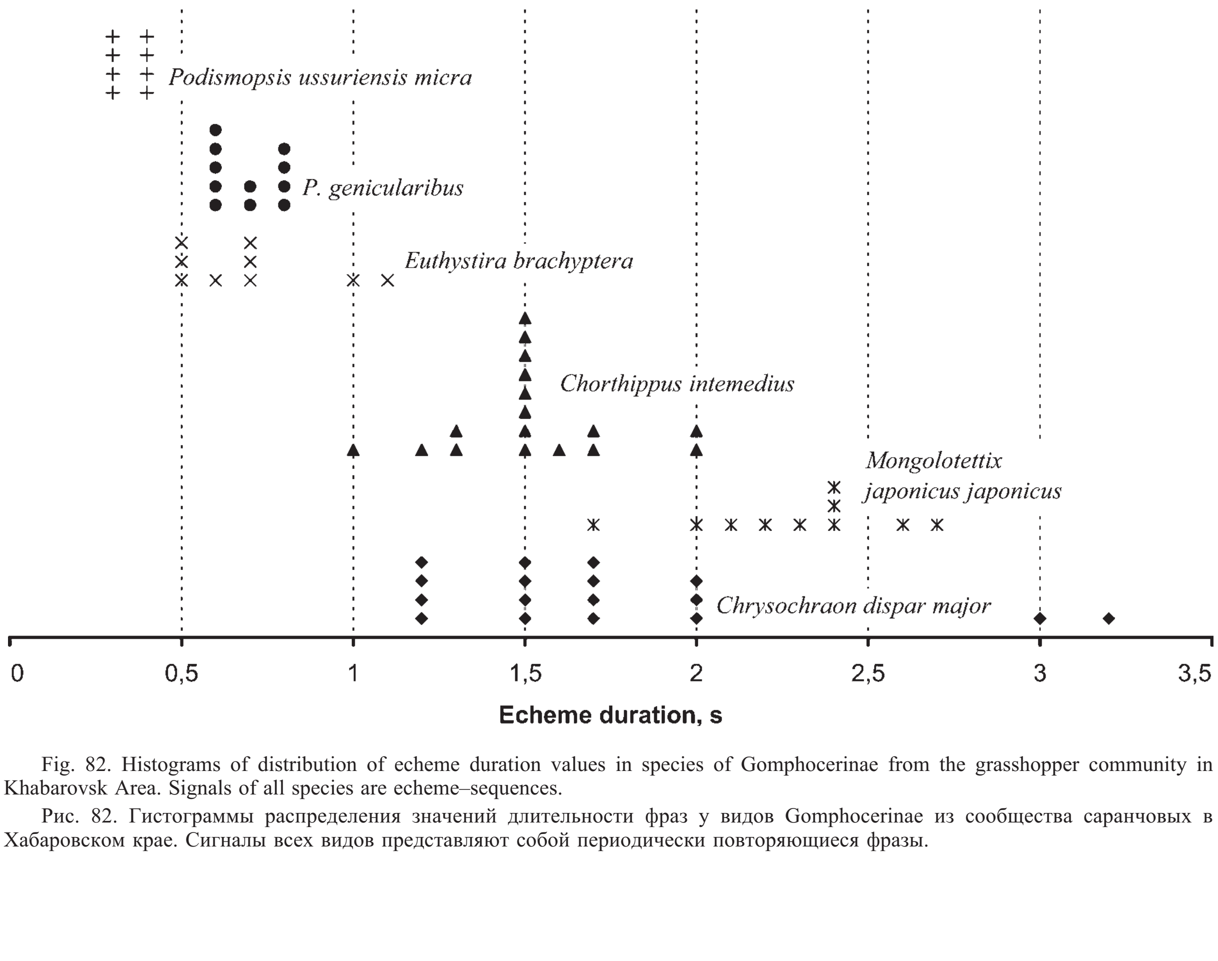


Fig. 82. Histograms of distribution of echeme duration values in species of Gomphocerinae from the grasshopper community in Khabarovsk Area. Signals of all species are echeme–sequences.

Рис. 82. Гистограммы распределения значений длительности фраз у видов Gomphocerinae из сообщества саранчовых в Хабаровском крае. Сигналы всех видов представляют собой периодически повторяющиеся фразы.

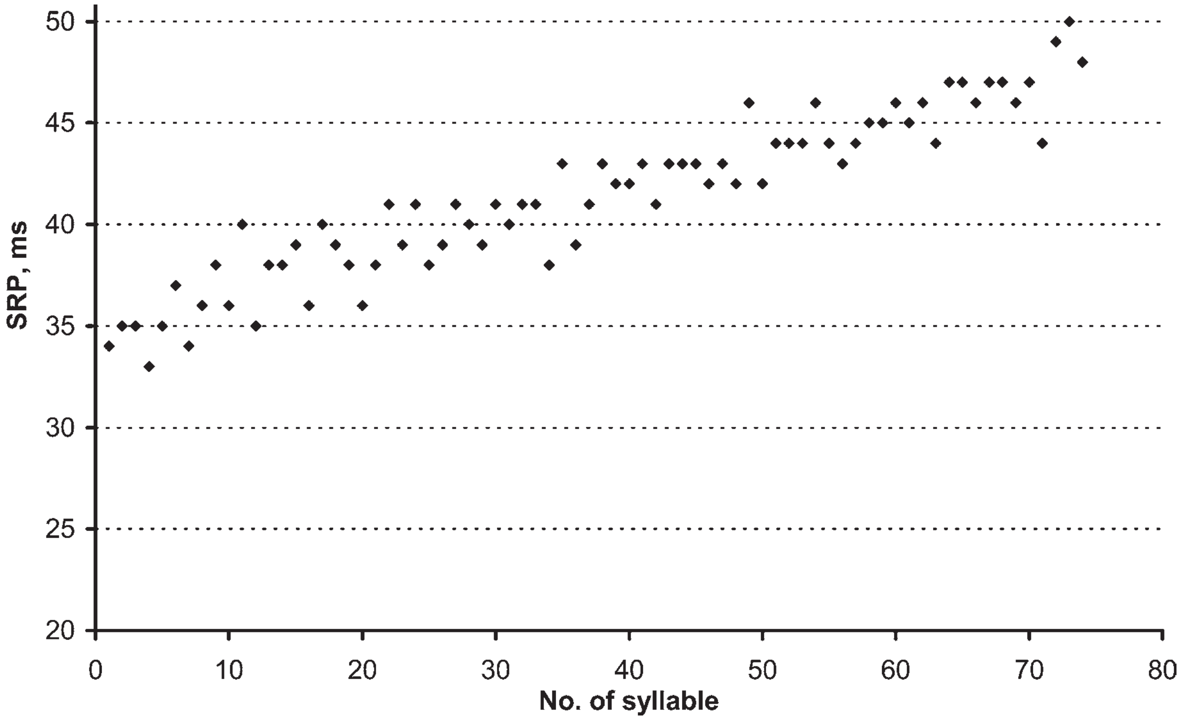


Fig. 83. The change of syllable repetition period (SRP) from the beginning to the end of the echeme of *Omocestus haemorrhoidalis*. The number of each syllable from the beginning of the echeme is laid off as abscissa, the SRP measured from the beginning of the syllable to the beginning of the next one is laid off as ordinate.

Рис. 83. Изменение периода повторения серий (ППС) от начала к концу фразы *Omocestus haemorrhoidalis*. По горизонтальной оси отложен порядковый номер каждой серии от начала фразы, по вертикальной — ППС, измеренный от начала этой серии до начала следующей.

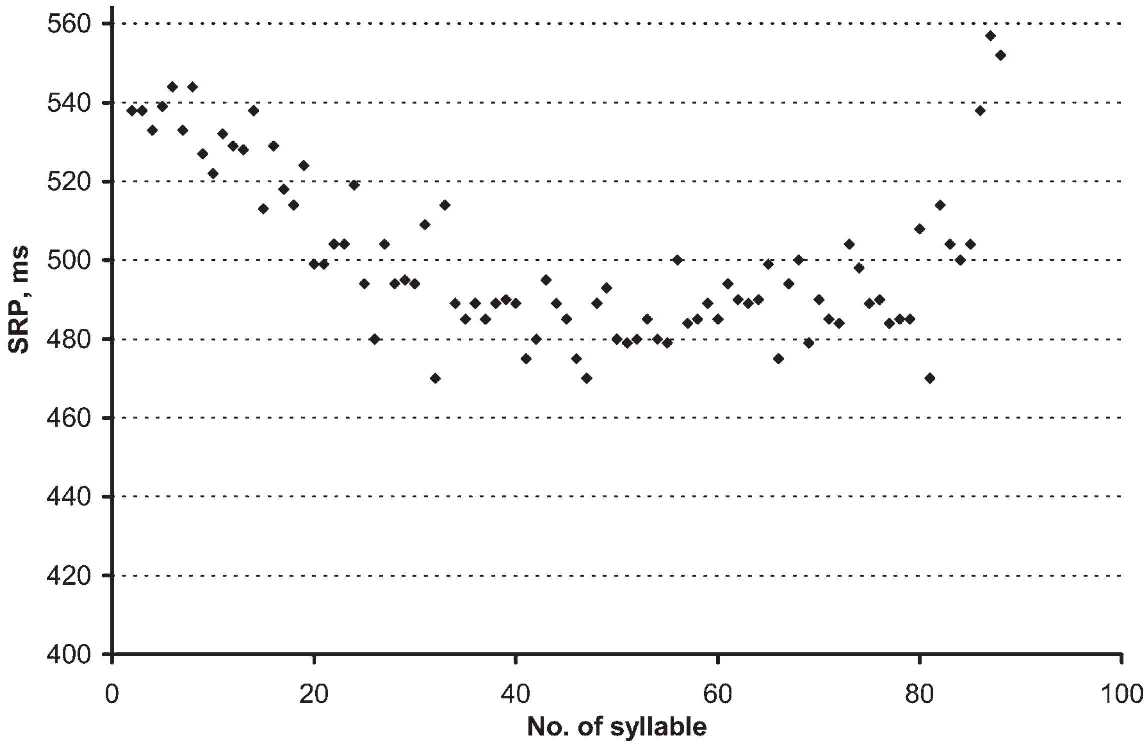


Fig. 84. The change of syllable repetition period (SRP) from the beginning to the end of the echeme of *Chorthippus apricarius*. The number of each syllable from the beginning of the echeme is laid off as abscissa, the SRP measured from the beginning of the syllable to the beginning of the next one is laid off as ordinate.

Рис. 84. Изменение периода повторения серий (ППС) от начала к концу фразы *Chorthippus apricarius*. По горизонтальной оси отложен порядковый номер каждой серии от начала фразы, по вертикальной — ППС, измеренный от начала этой серии до начала следующей.

histograms of SRP in the signals with similar temporal pattern of syllables are arranged in horizontal rows; the scheme at the right represents the pattern of syllables. It should be noted, that in certain communities each kind of syllable pattern is represented by single species.

First we consider each grasshopper community separately in order to reveal the pattern of segregation of communication channels.

The community in Irkutsk Area (No. 6 in the list above) includes six species: *Chorthippus karelini* (Uvarov, 1910), *Euthystira brachyptera* (Ocskay, 1826), *Podismopsis poppiusi* (Miram, 1907), *Stauroderus scalaris*, *Aeropus sibiricus* and *Omocestus viridulus*. All of them differ from each other in SRP almost without overlap of the ranges of this parameter (Fig. 92). For this reason it may appear that SRP is the only parameter providing segregation of communication channels and other characteristics of the signals are not necessary for their recognition. However, investigation of other communities shows that this impression is wrong.

The studied community in Moscow Area (No. 1 in the list) also includes six species: *Chorthippus parallelus* (Zetterstedt, 1821), *Ch. dorsatus*, *Chrysochraon dispar dispar* (Germar, 1835), *Ch. apricarius*, *G. biguttulus* and *O. viridulus*. Here the situation is more complex, than in the previous case (Fig. 93). In species with different structure of the signals the ranges of values of SRP can overlap fully (*G. biguttulus* and *Ch. dispar dispar*) or partially (*G. biguttulus* and *O. viridulus*). In addition, the species producing echemes consisting of two different parts, namely, *Ch. dorsatus* presents in the community (Figs 44–45). The ranges of SRP in both parts of its signal partially overlap with these of *Ch. parallelus* and *Ch. dispar dispar* respectively. Hence it follows that the differences in the pattern of echemes are quite sufficient for recognition of conspecific signal in spite of partial overlapping of the ranges of SRP and the similarity of general pattern of the song (echeme-sequences in the three species).

On the meadow with mesophytic vegetation in Rostov Area (locality No. 2) five species were found. These are *Ch. parallelus*, *Glyptobothrus mollis*, *Ch. apricarius*, *G. maritimus* (Mistshenko, 1951) and *Ch. macrocerus* (Fig. 94). Similarly with the community in Moscow Area, in species having different temporal structure of signals the ranges of SRP can overlap fully (*Ch. parallelus* and *G. maritimus*) or partially (*Ch. apricarius* and *Ch. mac-*

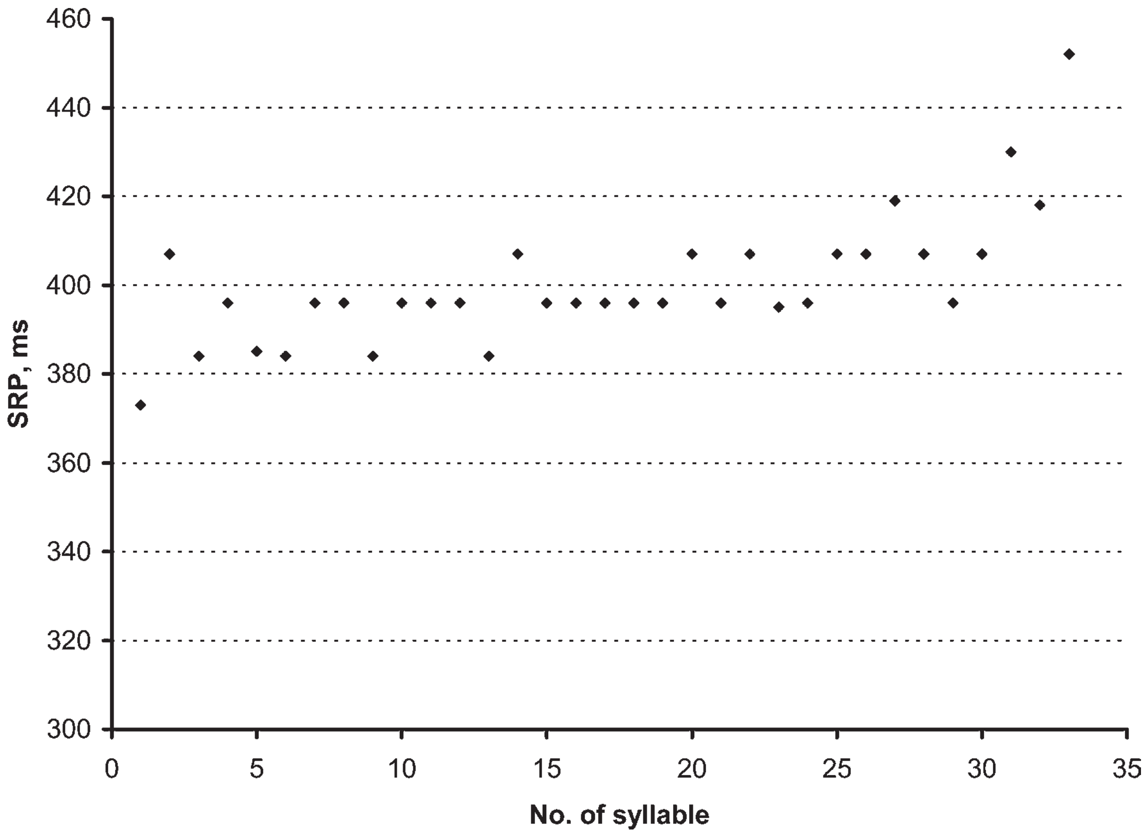


Fig. 85. The change of syllable repetition period (SRP) from the beginning to the end of the echeme of *Glyptobothrus mollis*. The number of each syllable from the beginning of the echeme is laid off as abscissa, the SRP measured from the beginning of the syllable to the beginning of the next one is laid off as ordinate.

Рис. 85. Изменение периода повторения серий (ППС) от начала к концу фразы *Glyptobothrus mollis*. По горизонтальной оси отложен порядковый номер каждой серии от начала фразы, по вертикальной — ППС, измеренный от начала этой серии до начала следующей.

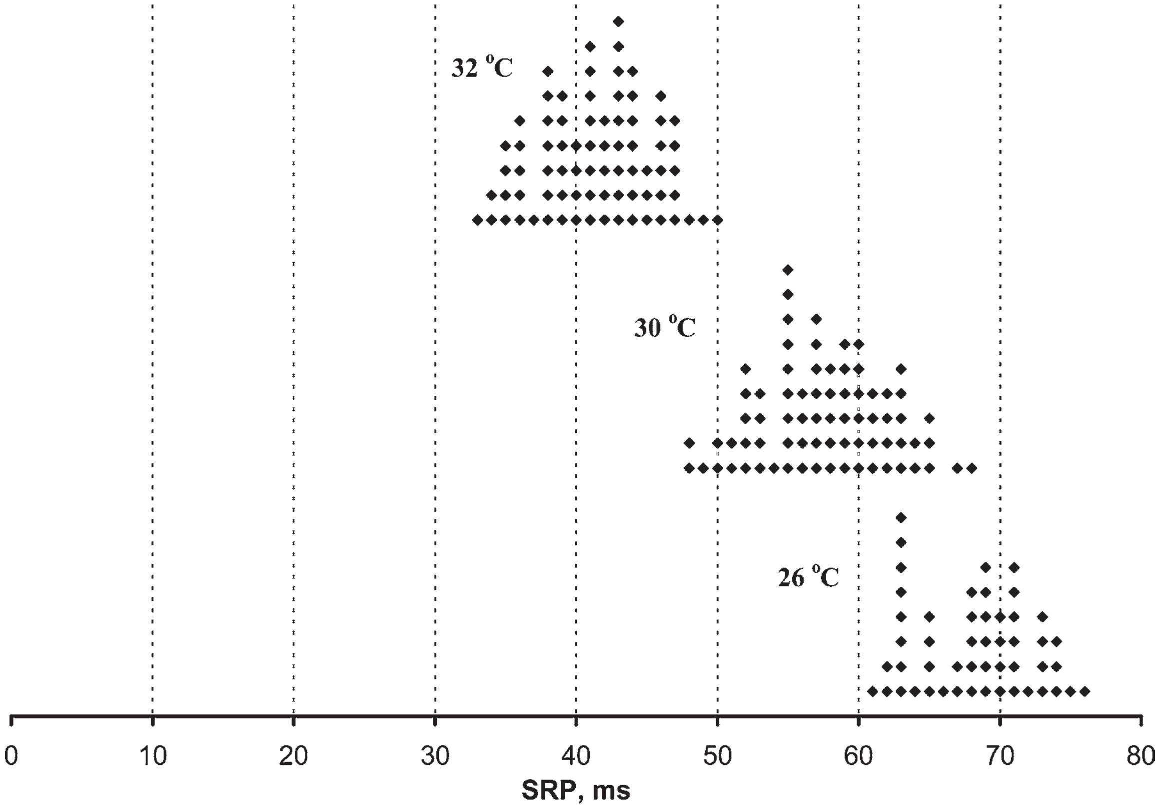


Fig. 86. Histograms of distribution of syllable repetition period in the song of *Omocestus haemorrhoidalis* at different temperatures.
Рис. 86. Гистограммы распределения периода повторения серий в сигналах *Omocestus haemorrhoidalis* при разных температурах.

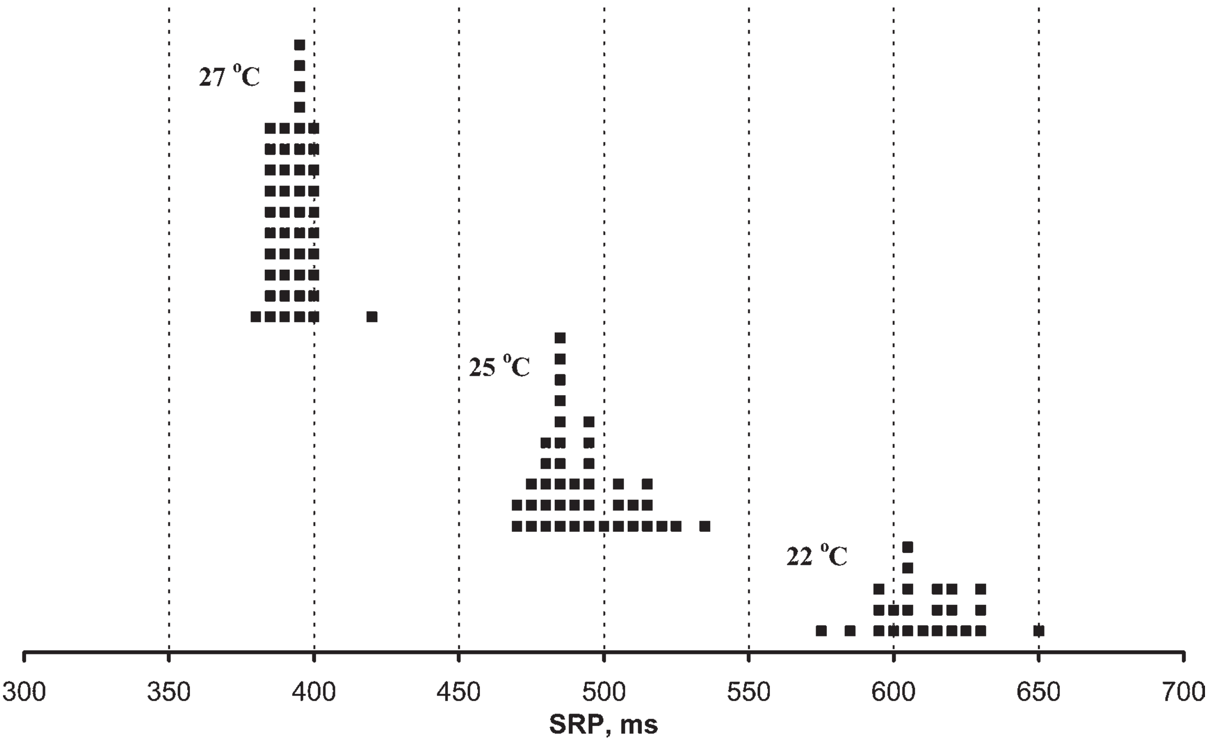


Fig. 87. Histograms of distribution of syllable repetition period in the song of *Chorthippus apricarius* at different temperatures.
Рис. 87. Гистограммы распределения периода повторения серий в сигналах *Chorthippus apricarius* при разных температурах.

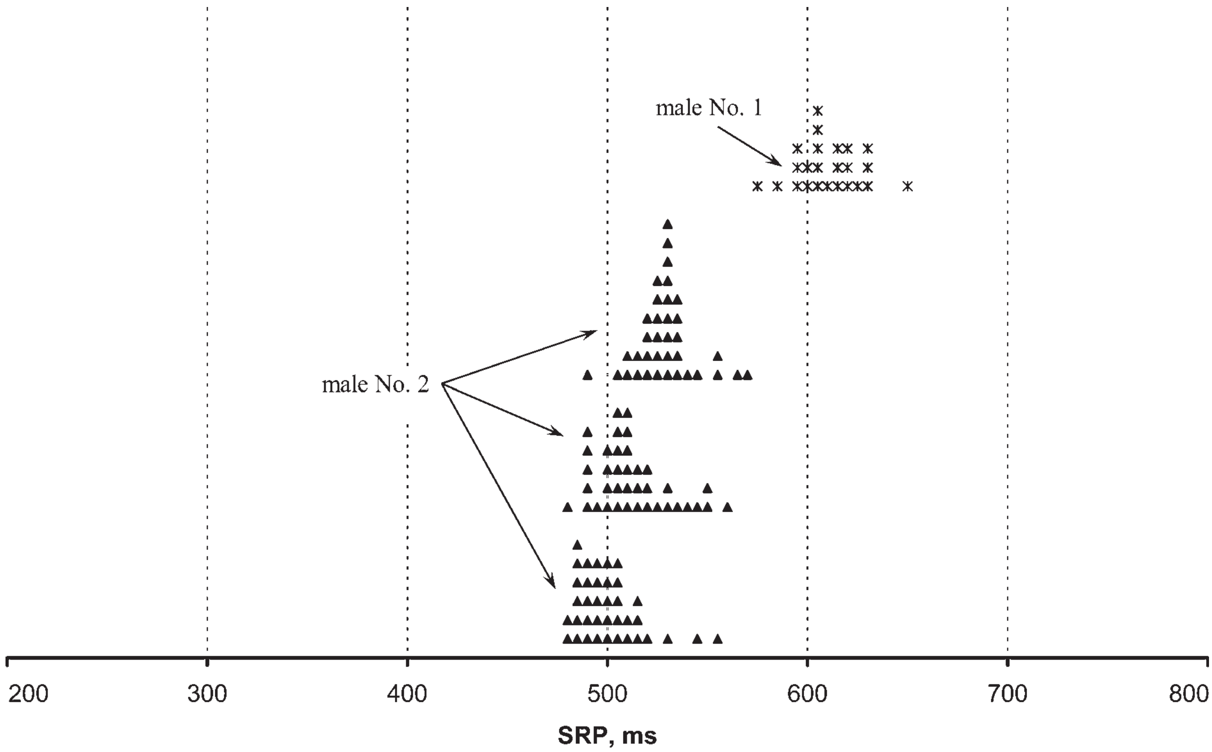


Fig. 88. Histograms of distribution of syllable repetition period (SRP) in the echemes of two males of *Chorthippus apricarius* from Moscow Area at the temperature 22°C. Data on each echeme are presented as a separate histogram. Probability of identity of SRP in different echemes according to Wilcoxon test P<0.05 (significant differences) in all cases.

Рис. 88. Гистограммы распределения периода повторения серий (ППС) в сигналах двух самцов *Chorthippus apricarius* из Московской обл. при температуре 22°C. Данные по каждому сигналы представлены в виде отдельной гистограммы. Вероятность идентичности ППС в разных сигналах по критерию Вилкоксона P<0,05 (достоверные различия) во всех случаях.

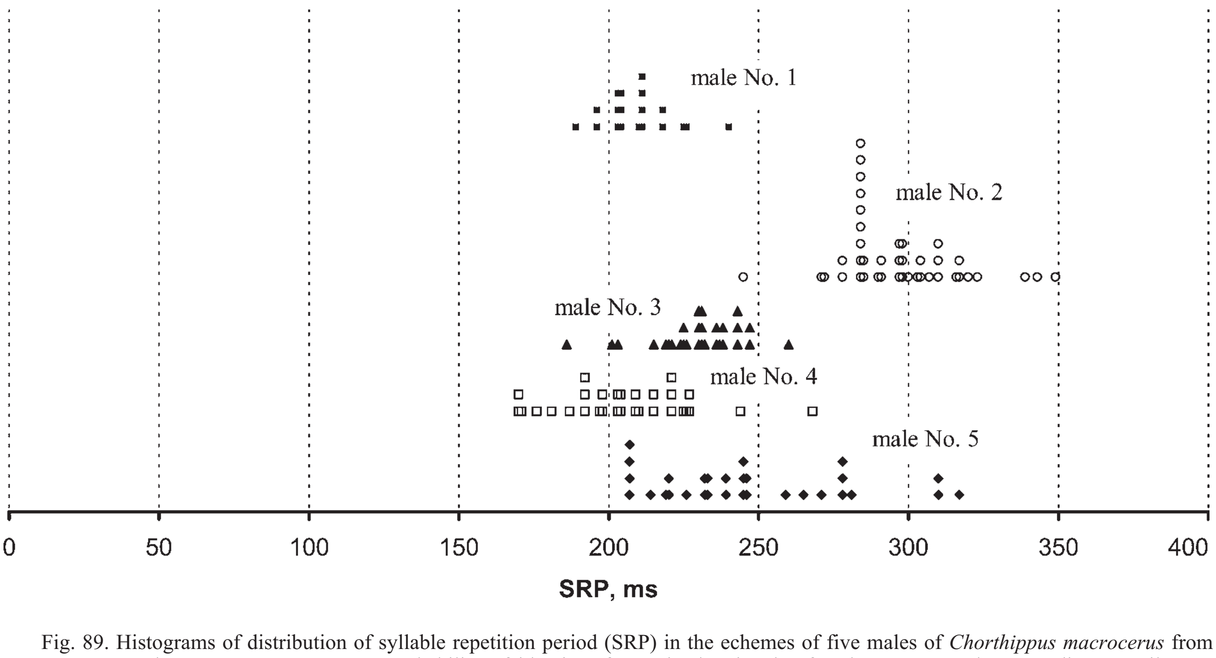


Fig. 89. Histograms of distribution of syllable repetition period (SRP) in the echemes of five males of *Chorthippus macrocerus* from Rostov Area at the temperature 29–30°C. Probability of identity of SRP in the signals of males Nos. 1 and 4 according to Wilcoxon test P=0.44, in the signals of males Nos. 3 and 5 P=0.05. In all other cases P<0.05 (significant differences).

Рис. 89. Гистограммы распределения периода повторения серий (ППС) в сигналах пяти самцов *Chorthippus macrocerus* из Ростовской обл. при температуре 29–30°C. Вероятность идентичности ППС в сигналах самцов № 1 и 4 по критерию Вилкоксона P=0,44, в сигналах самцов № 3 и 5 P=0,05. Во всех остальных случаях P<0,05 (достоверные различия).

rocerus). On the other hand, in species producing signals with similar pattern (*G. maritimus* and *Ch. macrocerus*, Figs 7–8 and 15–16 respectively) the ranges of SRP overlap only in extreme values. It is notable that the values of SRP in the songs of *G. mollis* and *Ch. apricarius* overlap only to a small extent despite differences in the inner structure of syllables (Figs 20 and 22).

The community of the glades in the forest shelterbelts in Rostov Area (No. 3 in the list) includes five species (*Euchorthippus pulvinatus* (Fischer-Waldheim, 1846), *Ch. apricarius*, *Omocestus minutus* (Brullé, 1832), *G. maritimus* and *Chorthippus vagans* (Eversmann, 1848)) and exhibit the same regularities (Fig. 95). The signals of different types have almost the same ranges of SRP (in *E. pulvinatus* and *O. minutus*), whereas the signals of the same type (in *G. maritimus* and *Ch. vagans*) overlap in this parameter only to a small extent. It should be pointed out that in this community *Ch. macrocerus* is replaced by *Ch. vagans* having the same temporal pattern of the song and SRP.

The highest diversity of Gomphocerinae (11 species) was found in steppe locality in Rostov Area (No. 4 in the list). Similarly, in this community species producing the signals of the same type occupy different ranges of SRP, whereas in the signals belonging to different types this parameter sometimes have the same values (Fig. 96).

The community of the salted land in Volgograd (locality No. 5) is similar with the previous one in species composition. Three steppe species (*Stenobothrus nigromaculatus* (Herrich-Schäffer, 1840), *O. petraeus* and *Ch. macrocerus)* are absent from this community and *Ch. parallelus* is replaced by *Eremippus costatus* Tarbinski, 1927 producing the signals with the same SRP and the type of temporal pattern (Fig. 97).

The community in Khabarovsk Province (locality No. 7) is remarkable due to the fact that the signals of all its members are echeme-sequences (Fig. 98). Moreover, in *Ch. intermedius* the echemes sometimes consist of two different parts (Figs 58–61), and *P. genicularibus* can produce syllables both with and without gaps (Figs 46–49). For this reason two histograms are presented on the scheme for each of these species. Five species producing syllables without gaps are arranged on the SRP axis almost without overlapping. Only in the second (facultative) part of echemes of *Ch. intermedius*

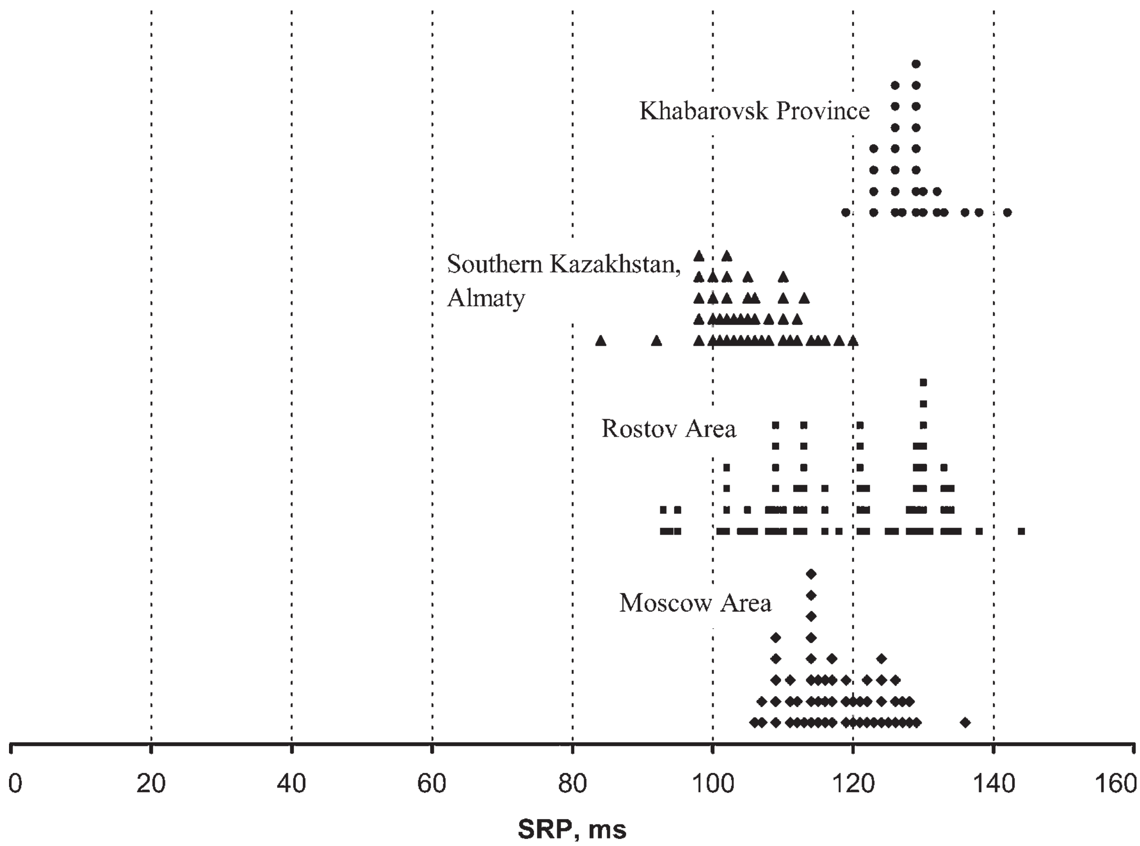


Fig. 90. Histograms of distribution of syllable repetition period (SRP) in the songs of *Chrysochraon dispar* from different localities at the temperature 28–31°C. Probability of identity of SRP in the signals of males from Moscow Area and Rostov Area according to Wilcoxon test P=0.50. In all other cases P<0.05 (significant differences).

Рис. 90. Гистограммы распределения периода повторения серий (ППС) в сигналах самцов *Chrysochraon dispar* из разных географических точек при температуре 28–31°C. Вероятность идентичности ППС в сигналах самцов из Московской и Ростовской областей по критерию Вилкоксона P=0,50. Во всех остальных случаях P<0,05 (достоверные различия).

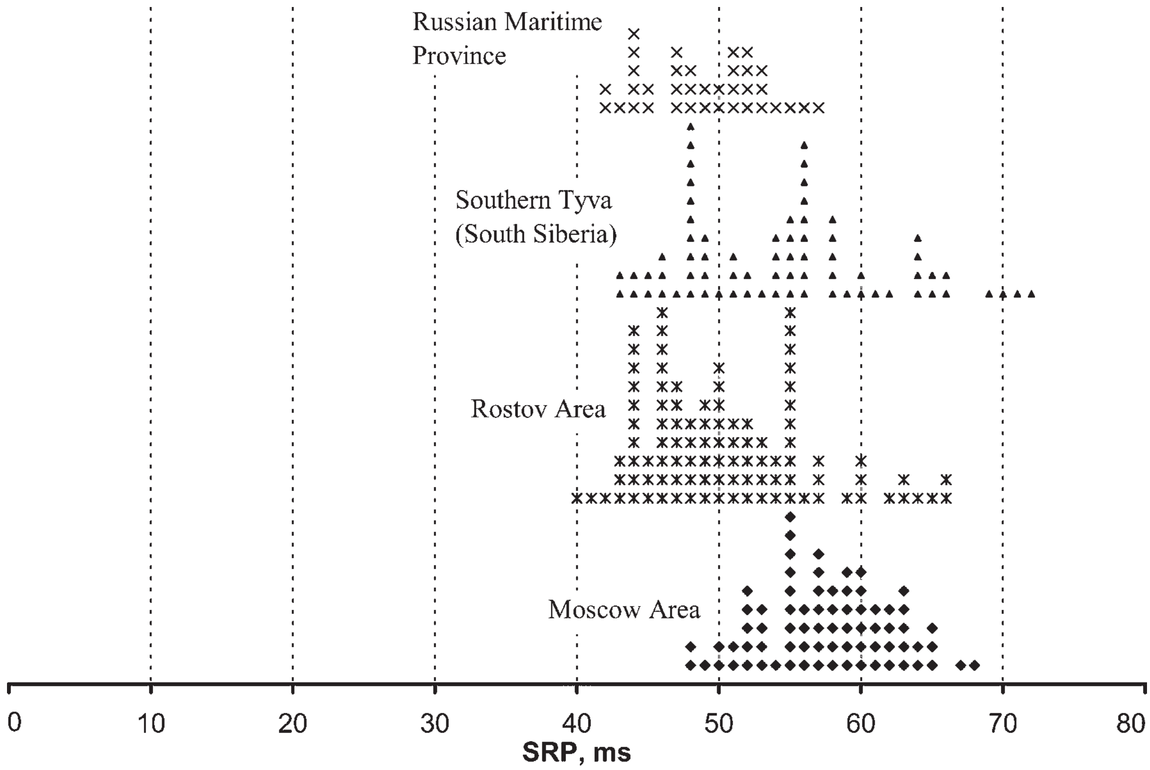


Fig. 91. Histograms of distribution of syllable repetition period (SRP) in the songs of *Omocestus haemorrhoidalis* from different localities at the temperature 30–32°C. Probability of identity of SRP in the signals of males from Rostov Area and Southern Tyva according to Wilcoxon test P=0.65, in the signals of males from Russian Maritime Province and Southern Tyva P= 0.76, in the signals of males from Russian Maritime Province and Rostov Area P=0.28. In all other cases P<0.05 (significant differences).

Рис. 91. Гистограммы распределения периода повторения серий (ППС) в сигналах самцов *Omocestus haemorrhoidalis* из разных географических точек при температуре 30–32°C. Вероятность идентичности ППС в сигналах самцов из Ростовской области и Южной Тувы по критерию Вилкоксона P=0,65, в сигналах самцов из Приморья и Южной Тувы P=0,76, в сигналах самцов из Приморья и Ростовской области P=0,28. Во всех остальных случаях P<0,05 (достоверные различия).

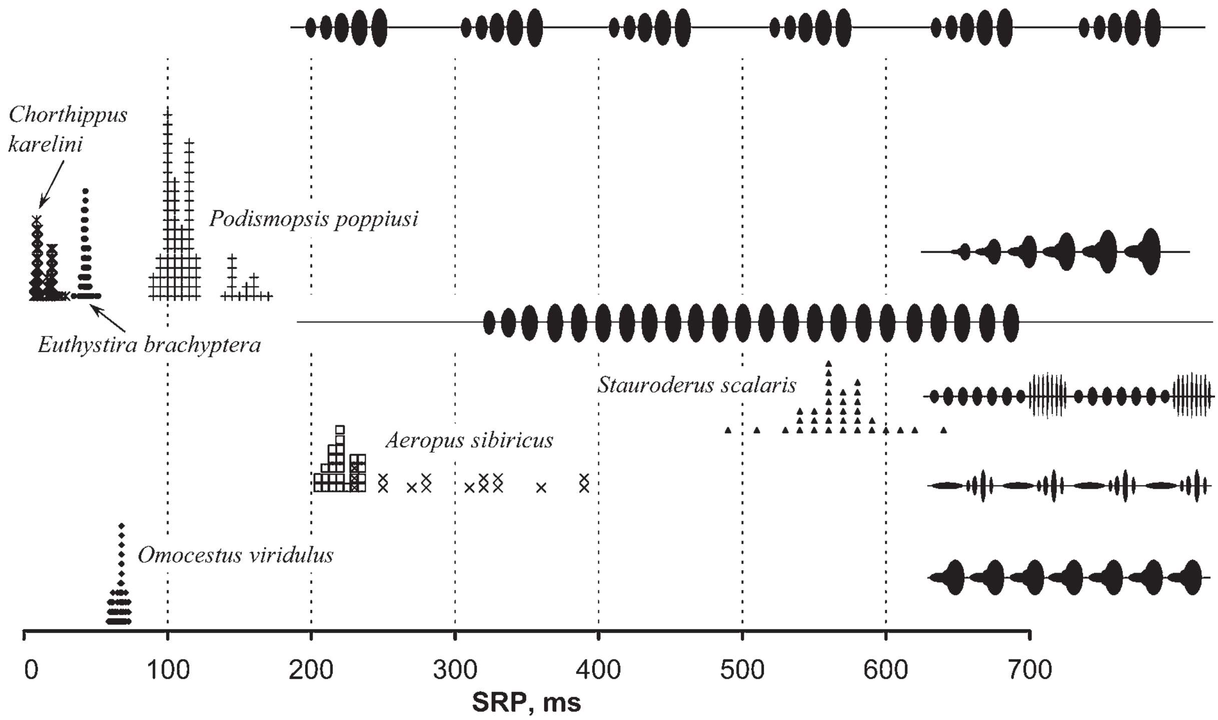


Fig. 92. Histograms of distribution of syllable repetition period (SRP) in the songs of grasshoppers from the community on the polydominant glade on the bank of Uk River in Irkutsk Area at the temperature 28–31°C. Probability of identity of SRP in the signals of different species according to Wilcoxon test P<0.05 (significant differences) in all cases.

Рис. 92. Гистограммы распределения периода повторения серий (ППС) в сигналах симпатрических видов саранчовых, населяющих разнотравную поляну на берегу реки Ук в Иркутской области, при температуре 28–31°C. Вероятность идентичности ППС в сигналах разных видов по критерию Вилкоксона P<0,05 (достоверные различия) во всех случаях.

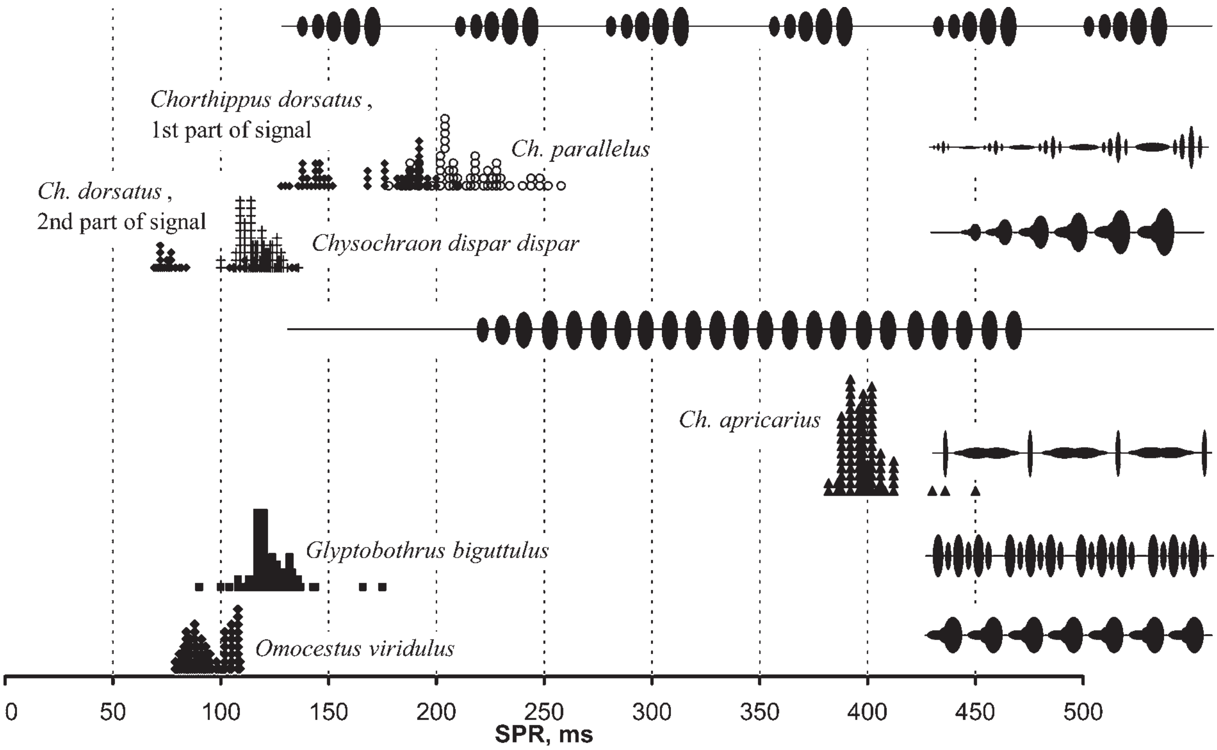


Fig. 93. Histograms of distribution of syllable repetition period (SRP) in the songs of grasshoppers from the community on the meadow with mesophytic vegetation in Moscow Area at the temperature 27–30°C. Probability of identity of SRP in the signals of different species according to Wilcoxon test P<0.05 (significant differences) in all cases.

Рис. 93. Гистограммы распределения периода повторения серий (ППС) в сигналах симпатрических видов саранчовых, населяющих луг с мезофитной растительностью в Московской области, при температуре 27–30°C. Вероятность идентичности ППС в сигналах разных видов по критерию Вилкоксона P<0,05 (достоверные различия) во всех случаях.

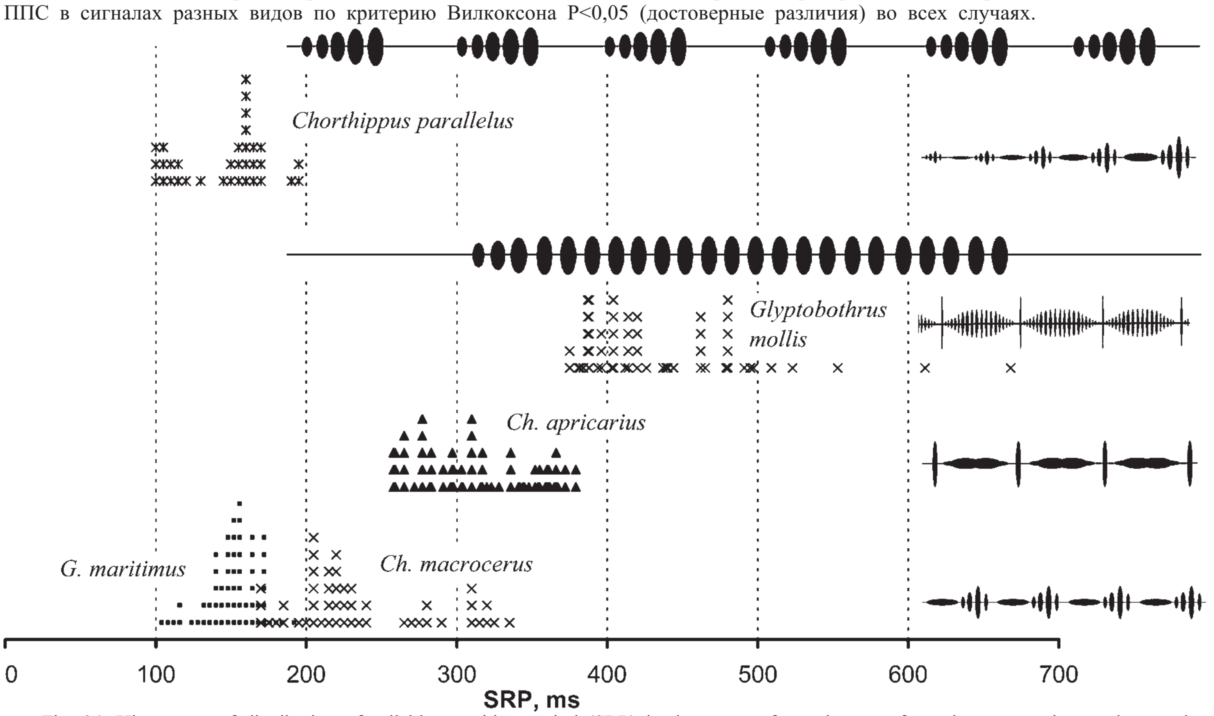


Fig. 94. Histograms of distribution of syllable repetition period (SRP) in the songs of grasshoppers from the community on the meadow with mesophytic vegetation on the edge of the field in Rostov Area at the temperature 27–30°C. Probability of identity of SRP in the signals of *Chorthippus parallelus* and *Glybtobothrus maritimus* according to Wilcoxon test P=0.87, in all other cases P<0.05 (significant differences).

Рис. 94. Гистограммы распределения периода повторения серий (ППС) в сигналах симпатрических видов саранчовых, населяющих луг с мезофитной растительностью на краю поля в Ростовской области, при температуре 27–30°C. Вероятность идентичности ППС в сигналах *Chorthippus parallelus* и *Glybtobothrus maritimus* по критерию Вилкоксона P=0,87, во всех остальных случаях P<0,05 (достоверные различия).

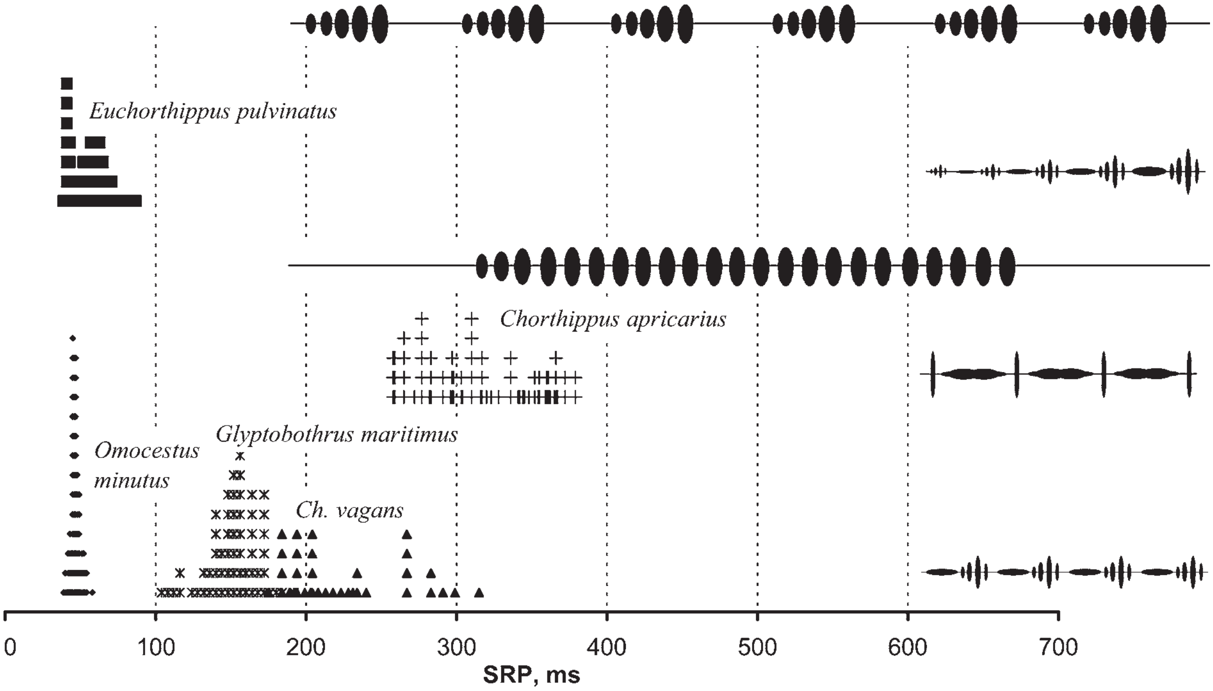


Fig. 95. Histograms of distribution of syllable repetition period (SRP) in the songs of grasshoppers from the community on the glades in the forest shelter–belts in Rostov Area at the temperature 27–30°C. Probability of identity of SRP in the signals of different species according to Wilcoxon test P<0.05 (significant differences) in all cases.

Рис. 95. Гистограммы распределения периода повторения серий (ППС) в сигналах симпатрических видов саранчовых, населяющих поляны в лесополосах в Ростовской области, при температуре 27–30°C. Вероятность идентичности ППС в сигналах разных видов по критерию Вилкоксона P<0,05 (достоверные различия) во всех случаях.

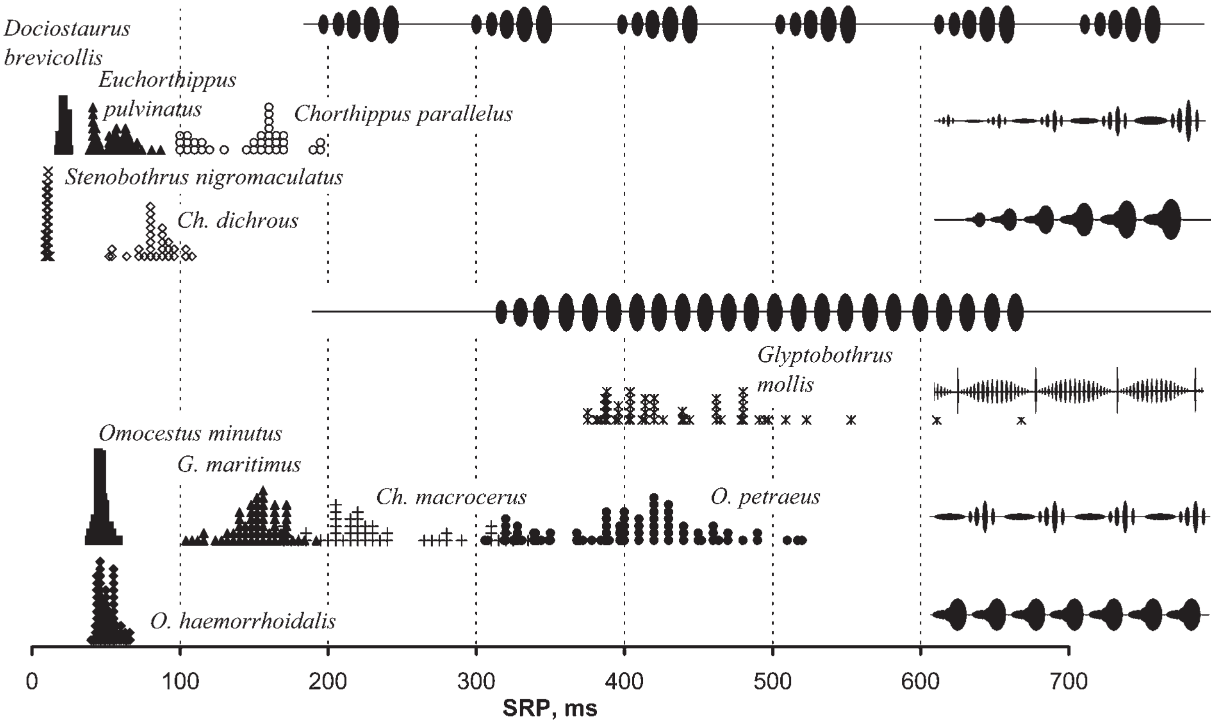


Fig. 96. Histograms of distribution of syllable repetition period (SRP) in the songs of grasshoppers from the community in the steppe dominated by *Stipa* sp. and *Festuca* sp. in Rostov Area at the temperature 27–30°C. Probability of identity of SRP in the signals of *Chorthippus parallelus* and *Glybtobothrus maritimus* according to Wilcoxon test P=0.87, in all other cases P<0.05 (significant differences).

Рис. 96. Гистограммы распределения периода повторения серий (ППС) в сигналах симпатрических видов саранчовых, населяющих типчаково-ковыльную степь в Ростовской области, при температуре 27–30°C. Вероятность идентичности ППС в сигналах *Chorthippus parallelus* и *Glybtobothrus maritimus* по критерию Вилкоксона P=0,87, во всех остальных случаях P<0,05 (достоверные различия).

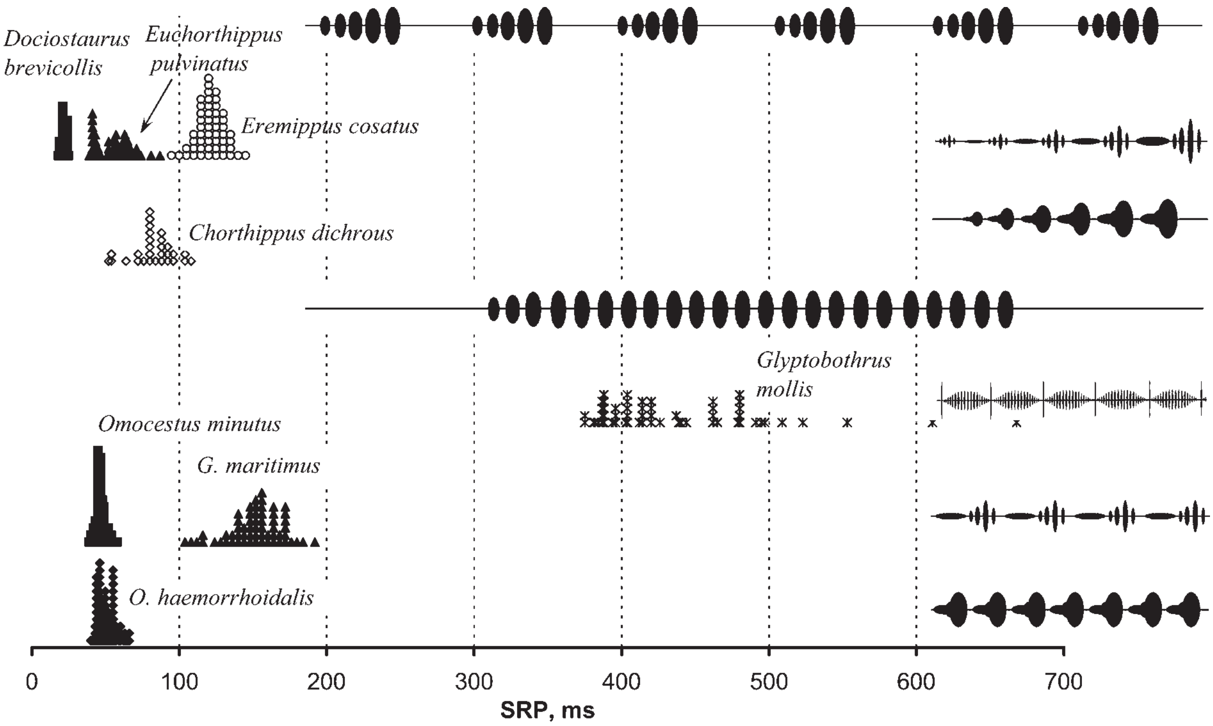


Fig. 97. Histograms of distribution of syllable repetition period (SRP) in the songs of grasshoppers from the community on the saline land in Volgograd at the temperature 27–30°C. Probability of identity of SRP in the signals of different species according to Wilcoxon test P<0.05 (significant differences) in all cases.

Рис. 97. Гистограммы распределения периода повторения серий (ППС) в сигналах симпатрических видов саранчовых, населяющих солончак в Волгограде, при температуре 27–30°C. Вероятность идентичности ППС в сигналах разных видов по критерию Вилкоксона P<0,05 (достоверные различия) во всех случаях.

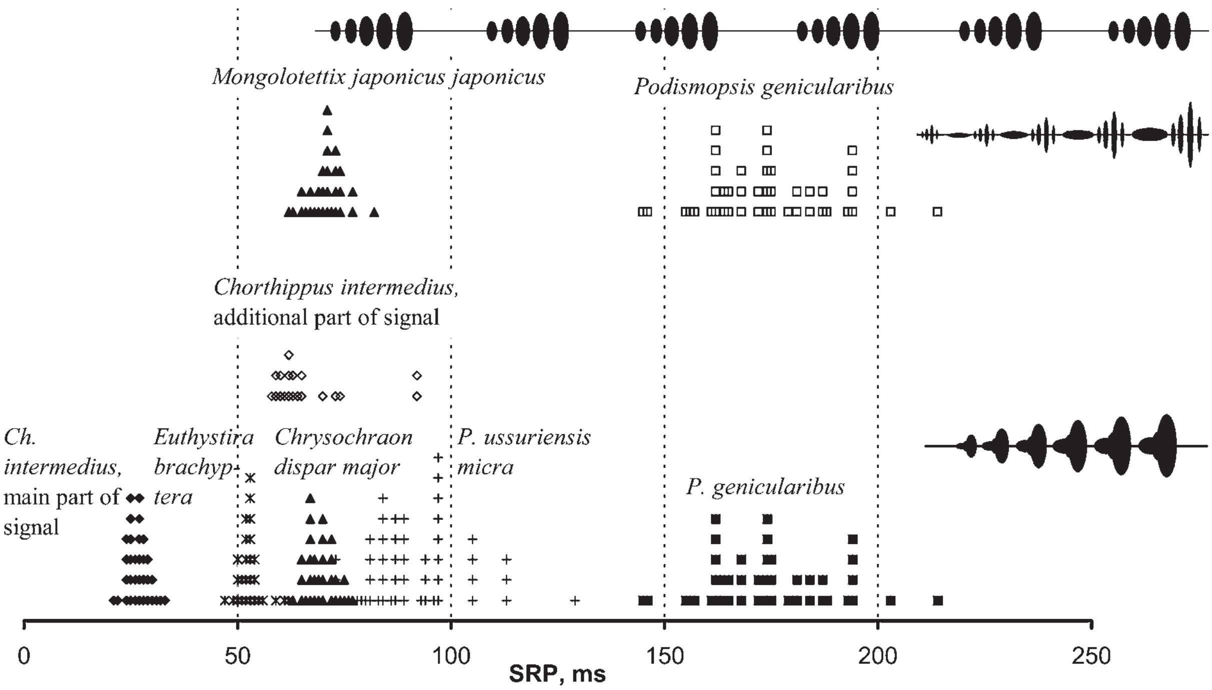


Fig. 98. Histograms of distribution of syllable repetition period (SRP) in the songs of grasshoppers from the community in the bog in Khabarovsk Province at the temperature 32–35°C. Probability of identity of SRP in the signals of *Chrysochraon dispar major* and *Mongolotettix japonicus japonicus* according to Wilcoxon test P=0.20, in all other cases P<0.05 (significant differences).

Рис. 98. Гистограммы распределения периода повторения серий (ППС) в сигналах симпатрических видов саранчовых, населяющих болото в Хабаровском крае, при температуре 32–35°C. Вероятность идентичности ППС в сигналах *Chrysochraon dispar major* и *Mongolotettix japonicus japonicus* по критерию Вилкоксона P=0,20, во всех остальных случаях P<0,05 (достоверные различия).

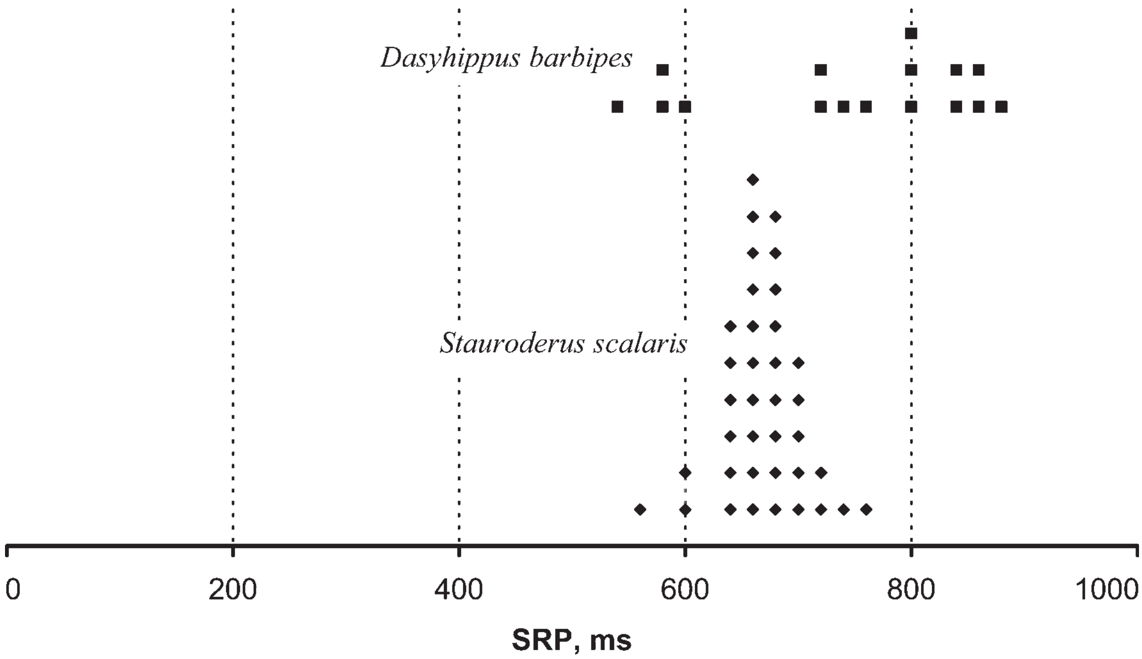


Fig. 99. Histograms of distribution of syllable repetition period (SRP) in the songs of *Stauroderus scalaris* and *Dasyhippus barbipes* from Buryatia at the temperature 35–36°C. Probability of identity of SRP according to Wilcoxon test $P<0.05$ (significant differences).

Рис. 99. Гистограммы распределения периода повторения серий (ППС) в сигналах *Stauroderus scalaris* и *Dasyhippus barbipes* из Бурятии при температуре 35–36°C. Вероятность идентичности ППС по критерию Вилкоксона $P<0{,}05$ (достоверные различия).

the range of SRP overlaps to some extent with these in the songs of other species.

From these data certain general conclusions regarding segregation of acoustic communication channels in the communities of Gomphocerinae can be drawn.

As is seen from the schemes (Figs 92–98), in sympatric species the signals differing from each other in general structure (single echemes or echeme-sequences) or/and in temporal pattern of syllables can occupy the same range of SRP. On the other hand, the signals similar both in general structure and in syllable pattern always differ from each other in SRP. The exceptions are the species producing echemes consisting of two different parts. In their songs the ranges of SRP sometimes can overlap considerably with these of sympatric species. This is true for both parts of the echeme of *Ch. dorsatus* (Fig. 93) and for the second part of the echeme of *Ch. intermedius* (Fig. 98). The same general rules were revealed in the grasshopper community studied by Bukhvalova [2006] in Southern Tyva (South Siberia).

As a result, the potential acoustic resources of the biotope may be imagined as a set of so-called acoustic niches. Acoustic niche is a part of the ecological niche as a whole; according to Bukhvalova [2006], it may be defined as the range of acoustic parameters of environment in which successful communication of the species is possible. In different biotopes the same acoustic niche can be occupied by different species, but two sympatric species cannot exist in the same niche.

Species producing signals with similar pattern and SRP, i.e. occupying the same acoustic niche were never found in the same community even though they may have certain differences in the structure of syllables. For instance, the songs of *Ch. macrocerus and Ch. vagans* somewhat differ from each other in syllable pattern (Figs 4 and 8 respectively), but are almost identical in other characteristics including SRP. It can be seen from Figs 94–96 that in Rostov Area these two species are formally sympatric, but replace each other in different biotopes. The same situation is observed in *Ch. parallelus* and *E. costatus* replacing each other in steppes and saline lands in the southern regions of European Russia (Figs 96–97). Their signals are similar in all formal parameters (echeme-sequences consisting of syllables with gaps and having the same SRP), but are not completely identical in temporal pattern (Figs 34–35 and 38–39).

S. scalaris and *D. barbipes* in the steppes of Transbaikalia provide one more example of this kind. Their signals are similar in temporal pattern (Figs 24 and 26) and have the same SRP (Fig. 99). In Buryatia, in the environs of Onokhoy village (about 60 km E of Ulan-Ude), where our observations were made, the former species was found only on the meadows on the banks of the river and the latter one inhabited steppes in river valley. The distance between these biotopes in certain places averaged no more than 10–20 m, nevertheless species under investigation were never found outside their habitats.

In certain species occupying the same acoustic niche not ecological, but geographical vicariation takes place. For example, in *S. miramae*, *Ch. macrocerus*

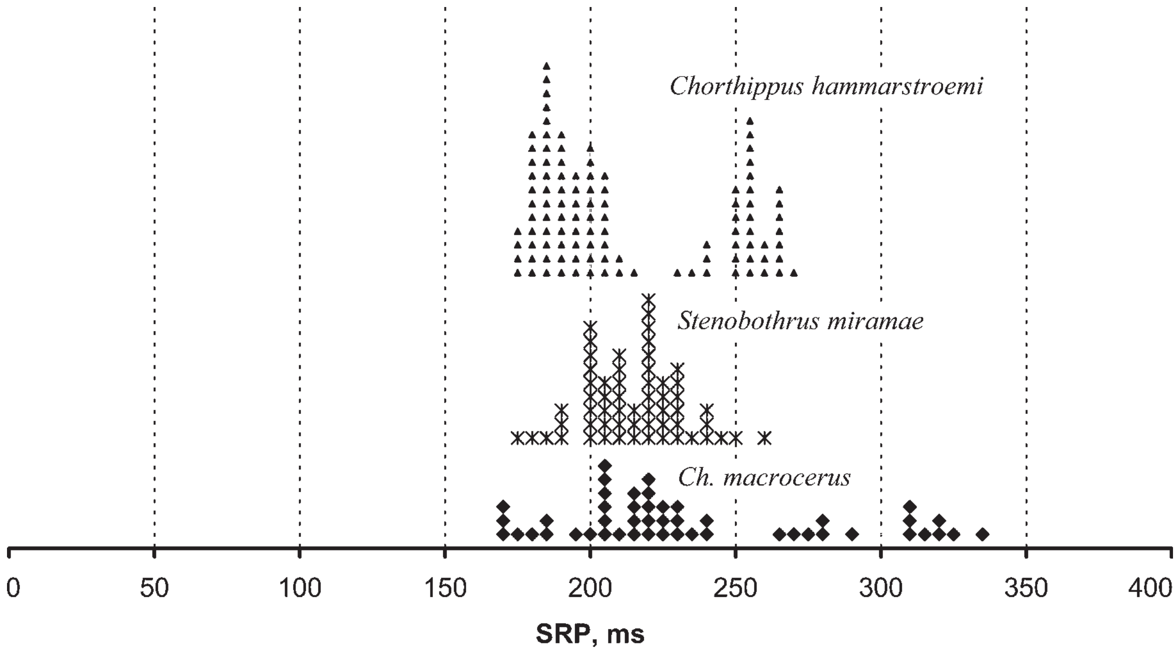


Fig. 100. Histograms of distribution of syllable repetition period (SRP) in the songs of *Chorthippus hammarstroemi* from Transbaikalia, *Stenobothrus miramae* from Crimea and *Ch. macrocerus* from Rostov Area at the temperature 28–32°C. Probability of identity of SRP in the signals of different species according to Wilcoxon test P<0.05 (significant differences) in all cases.

Рис. 100. Гистограммы распределения периода повторения серий (ППС) в сигналах *Chorthippus hammarstroemi* из Забайкалья, *Stenobothrus miramae* из Крыма и *Ch. macrocerus* из Ростовской области при температуре 28–32°C. Вероятность идентичности ППС в сигналах разных видов по критерию Вилкоксона P<0,05 (достоверные различия) во всех случаях.

and *Ch. hammarstroemi* temporal pattern of songs is quite similar (Figs 5–10) and SRP has the same values (Fig. 100). Thus the three species occupy the same acoustic niche, but avoid competition for communication channels due to allopatry. *S. miramae* was found in Crimea, in the south-eastern part of European Russia and in adjacent territories of Kazakhstan. The range of *Ch. macrocerus* includes southern part of European Russia, Caucasus, Transcaucasia, Asia Minor and Central Asia. However, we have not found it neither in the steppes of Kerchenskiy Peninsula (Crimea) nor in the environs of Orsk (Orenburg Area, South Urals), where *S. miramae* occurred. *Ch. hammarstroemi* is common in a steppe zone of South Siberia and in the southern part of the Russian Far East, but it is absent in European Russia; as a result its range does not overlap with these of two other species. Since all these species have wide distribution, it may be suggested that their ecological preferences are also rather wide. Thus it is quite possible that the reasons for their allopatry do not lie in a difference in ecological condition between localities, but in the similarity of their calling signals.

It can be assumed that the general structure of the signal (single echeme or echeme-sequence), syllable pattern and SRP are the most important characters, which can be used by insects for recognition of the song of conspecific mate. Even difference in one of these characters between two species provides segregation of their acoustic niches and thus forms precopulatory barrier of reproductive isolation. Consequently, such difference between sympatric forms inhabiting the same biotope testifies that they are good species. On the other hand, similarity of signal temporal pattern and SRP in allopatric forms is not an evidence of their synonymy.

Presently, there is a great body of literature on grasshopper communities in Palaearctic. It contains data on species composition of Gomphocerinae in many biotopes and plant associations in Russia, Kazakhstan, Central Asia, etc. [e.g. Pravdin, 1978]. However, acoustic interactions between the members of the communities were never taken into account in these studies in spite of the fact that the sounds produced by grasshoppers play a decisive role in their life. Recent studies show that competition for acoustic transmission channels between different species sometimes is no less strong as for other resources [Riede, 1996]. In certain cases it can influence the species composition of the community and thus affect the distribution of the species.

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